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Vol. XLIV

No. 1

THE
BOTANICAL GAZETTE

July 1907

Editors: JOHN M. COULTER and CHARLES R. BARNES

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EDITORS:
JOHN MERLE COULTER AND CHARLES REID BARNES

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ERRATA

Vol. **43**: for errata see note **44**:80.

P. 33, for last two lines read

Rhexia mariana

FIG. 16.—Transverse section of ventral epidermis of leaf. ×320.

P. 99, citation 6, for uredospores read uredospore.

P. 151, line 2 from bottom, for Immunetäts read Immunitäts.

P. 264, first item under Table V, for Nacl read NaCl.

P. 312, footnote 5, for Bieträge read Beiträge.

P. 313, line 1 from below, footnotes, for 197 read 177.

P. 397, footnote 23, for Invgarson read Ingvarson.

P. 399, line 2 and footnote 33, for PRIESTLY read PRIESTLEY.

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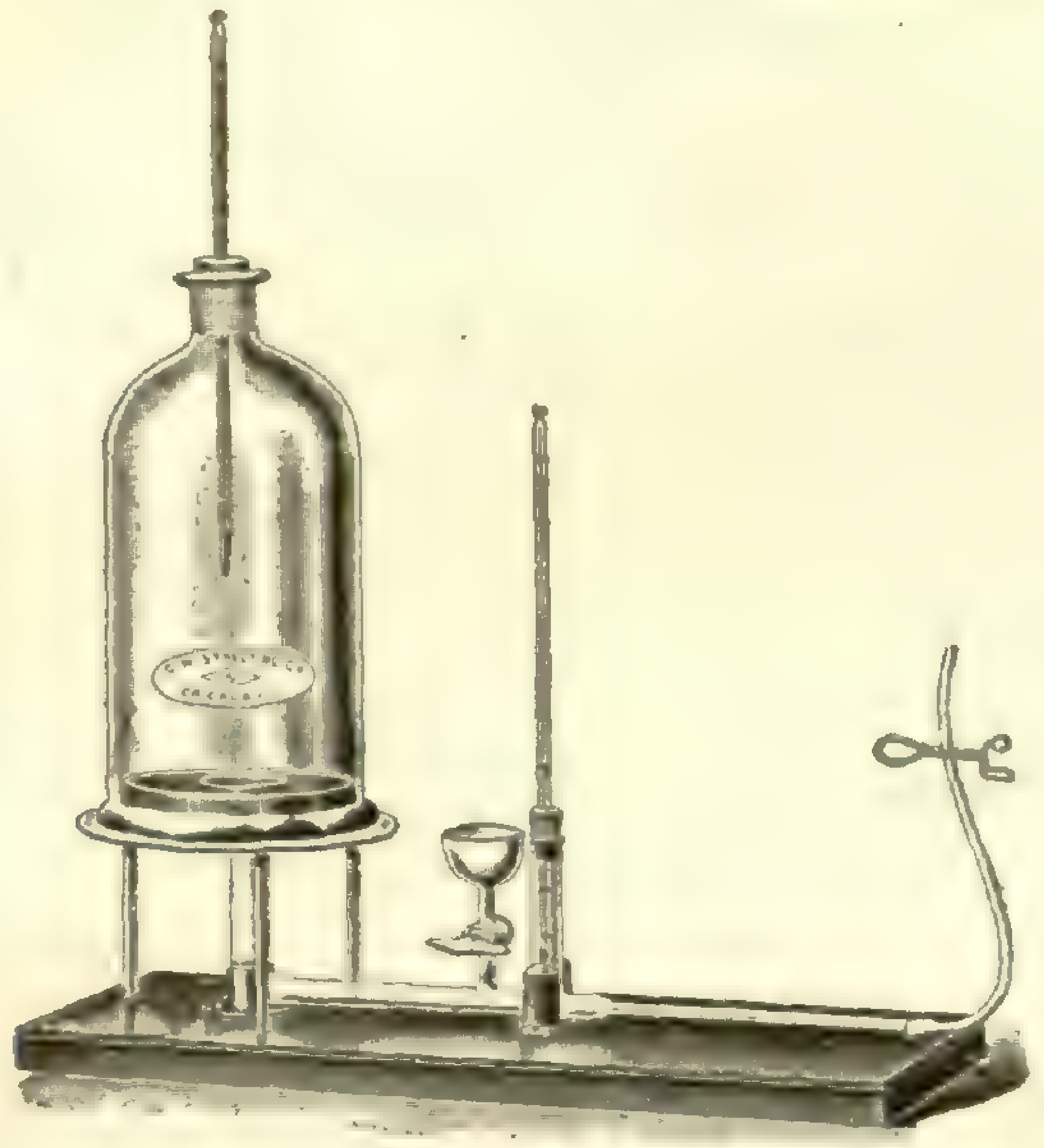

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VOLUME XLIV NUMBER 1

BOTANICAL GAZETTE

JULY 1907

HYBRIDIZATION AND GERM CELLS OF OENOTHERA MUTANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCIII

REGINALD RUGGLES GATES

Since my previous paper[1] went to press, in which were described the conditions of abortive pollen development in *O. lata*, as well as some of the stages in pollen development in the *O. Lamarckiana* hybrid obtained by crossing *O. lata* with *O. Lamarckiana* pollen, further investigations have placed in a new light the situation in regard to the number of chromosomes in the Oenothera mutants and hybrids studied. The further facts obtained have disclosed quite a different condition from the one anticipated, and one which is at present wholly inexplicable, and apparently quite unique so far as chromosomes are concerned, though it is to be expected that fuller knowledge of the facts will bring an explanation of the situation. Since the facts, so far as known at present, appear to be most directly concerned with Oenothera hybrids, a brief account of the forms of hybridization among the Oenothera mutants, as developed by the very extensive hybridizing experiments of DEVRIES,[2] will first be necessary.

FORMS OF OENOTHERA HYBRIDS

In general, DEVRIES' experiments appear to disclose at least three main forms or types of hybridization in the Oenothera mutants: (1) hybrids between a mutant and the parent *O. Lamarckiana;*

---

[1] GATES, R. R., Pollen development in hybrids of *Oenothera lata* × *O. Lamarckiana*, and its relation to mutation. BOT. GAZETTE **43**:81–115. *pls. 2–4.* 1907.

[2] DEVRIES, HUGO, Die Mutationstheorie, Vol. II. 1903.

(2) hybrids between two mutants; (3) ordinary Mendelian hybrids, which appear in some of the mutant crosses. These can only be considered as general tendencies, however, for the results vary widely in many of the crosses, both in the number and the percentage of the types appearing. DeVries has also been able to vary the results experimentally in a number of cases. Crosses in which a mutant is involved he calls mutation hybrids (*Mutationskreuzungen*), and hybrids of exactly this character do not occur, so far as I know, in any other genus of plants or animals.

The conspicuous types of hybridization in Oenothera are as follows: When *O. Lamarckiana* is crossed with a mutant, in the case of several of the forms DeVries experimented upon, a hybrid is produced which splits, but differs from a typical Mendelian hybrid in three respects. (1) A heterozygote, showing only the characters of the dominant parent, and containing the recessive characters latent, is not formed in the first hybrid generation, but instead the two parent forms are produced. (2) The proportions of the offspring are not always about 3:1 as in a Mendelian hybrid, but the percentage of plants having the recessive characters (the mutants are recessive to the parent *O. Lamarckiana*) often fluctuates between 0 and 50 per cent., or even with wider range. This distinction is believed to be less important, as fluctuations in the percentage of the forms are known to occur in some Mendelian hybrids. (3) A still more striking difference is that, while in a Mendelian hybrid two-thirds of the dominant plants continue to split in the proportions of 3:1 in successive generations, both the forms produced in a mutation hybrid, or cross of *O. Lamarckiana* with a mutant, breed true and show no splitting. There is thus no external evidence that crossing has ever occurred. This type of hybrid appears when *O. lata*, *O. nanella*, or *O. rubrinervis* is crossed with *O. Lamarckiana*. The following diagram will make clear the distinctions between this and an ordinary Mendelian hybrid. *A* represents the characters of *O. Lamarckiana* in *fig. 1*, and of the dominant parent in *fig. 2*. *B* represents the characters of a mutant in *fig. 1*, and of the recessive parent in *fig. 2*.

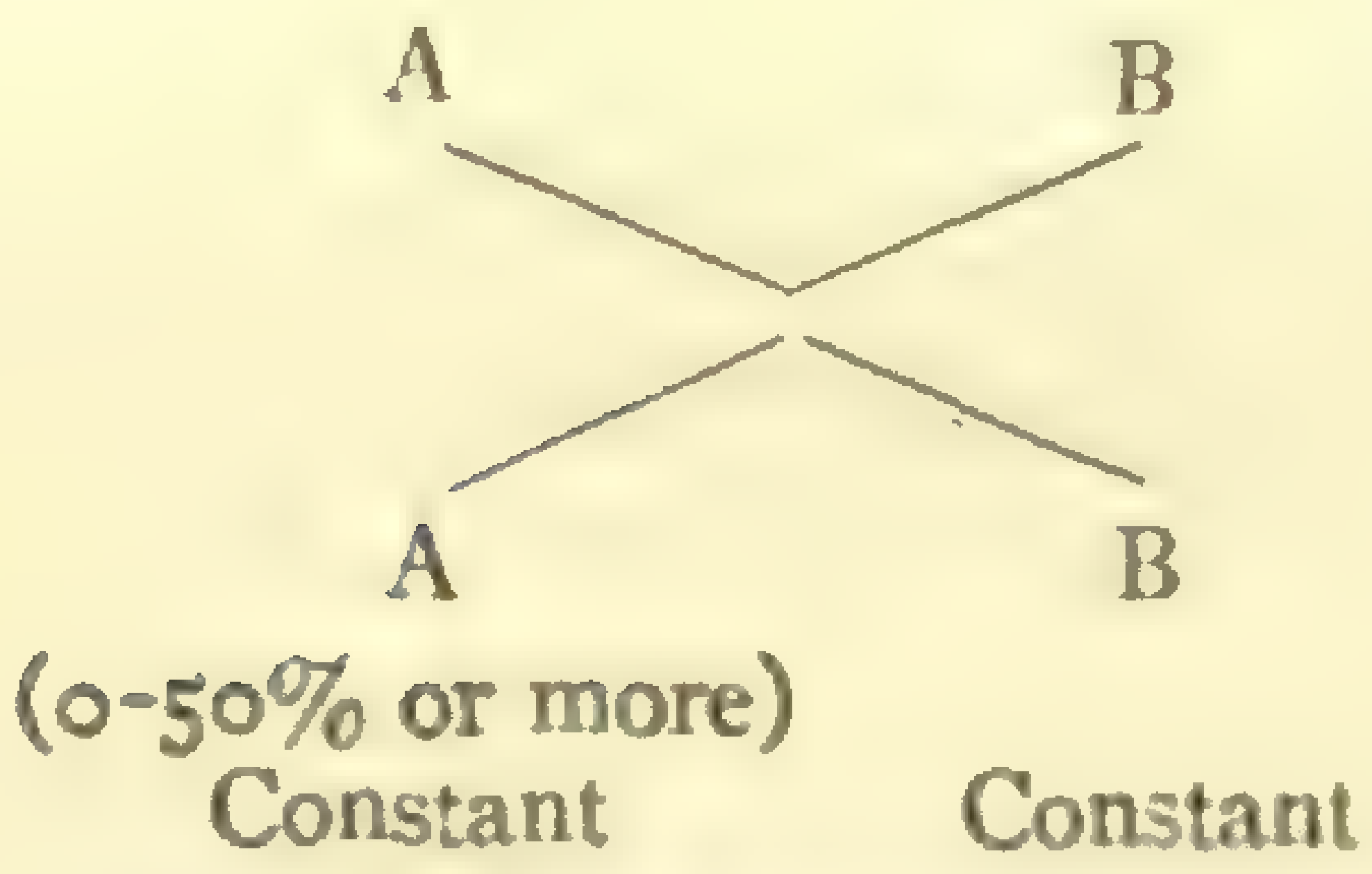

Fig 1.—Mutation hybrid

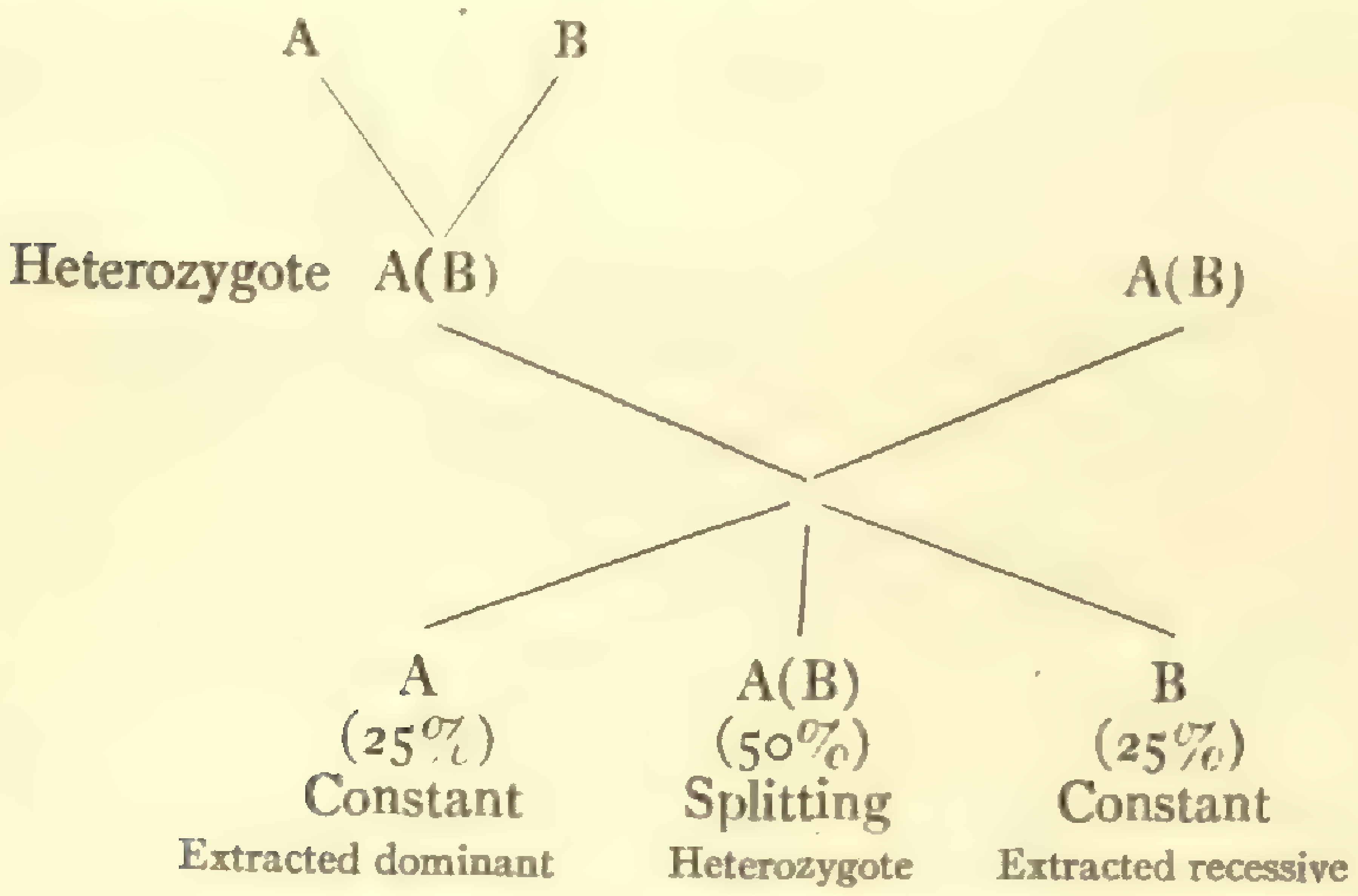

FIG. 2.—Mendelian hybrid

Two significant exceptions to this form of hybrid among the mutants are found in *O. brevistylis* and *O. laevifolia*, which never appeared as mutants in DEVRIES' cultures, although he believes them to have formerly mutated from *O. Lamarckiana*. They form with *O. Lamarckiana* ordinary Mendelian hybrids.

The fact that the percentage of a mutant appearing in a cross can be experimentally varied in different ways is also of importance in this connection. Thus the percentage of the parent forms appearing in a cross varies with the position on the stem of the particular flowers crossed. The plants bloom from below upward on the stem, and DEVRIES observed that after the first few weeks of blooming there is a steady and marked decrease in the size of the flowers blooming, until at the close of the season they are but little larger than those of *O. biennis*. I have observed the same thing in my own cultures from seeds of DEVRIES at Woods Hole, Mass. At the end of September many of the plants were still blooming vigorously at the top, and the flowers were little if any larger than those of *O. biennis*. When pollen from a mutant is used to cross with *O. Lamarckiana*, if it is obtained from the earlier flowers of the season, that is from the larger and more vigorous flowers which are lower on the stem, the heredity-coefficient,[3] or percentage of the mutant appearing in a cross, will be larger than if later and smaller flowers are used. Similarly the heredity-coefficient (*Erbzahl*) of flowers on the side branches of *O. lata* when crossed with *O. Lamarckiana* is said to be less than that of flowers on the main axis (DEVRIES *l. c.* **2**:416). The heredity-coefficient of a mutant, when the large earlier flowers are used, appears to be a fairly constant quantity and to be usually or at least frequently near the Mendelian ratio, though it may often fluctuate in individual crosses of flowers from 0 to about 50 per cent. Thus the heredity-coefficient of *O. lata* is often 21–24 per cent., and that of *O. nanella* is practically the same. This percentage is said to remain about the same from generation to generation and to be independent of the pollen parent; but in crosses of single flowers the percentage may vary widely. Thus 39 crosses of *O. Lamarckiana* flowers were made with *O. nanella* pollen, and the seeds from the different flowers sown separately. The proportions of *O. nanella* obtained, that is the heredity-coefficient, varied from 1 to 48 per cent., the average for the total number of 3768 seedlings being about 17 per cent. (DEVRIES *l. c.* **2**:408).

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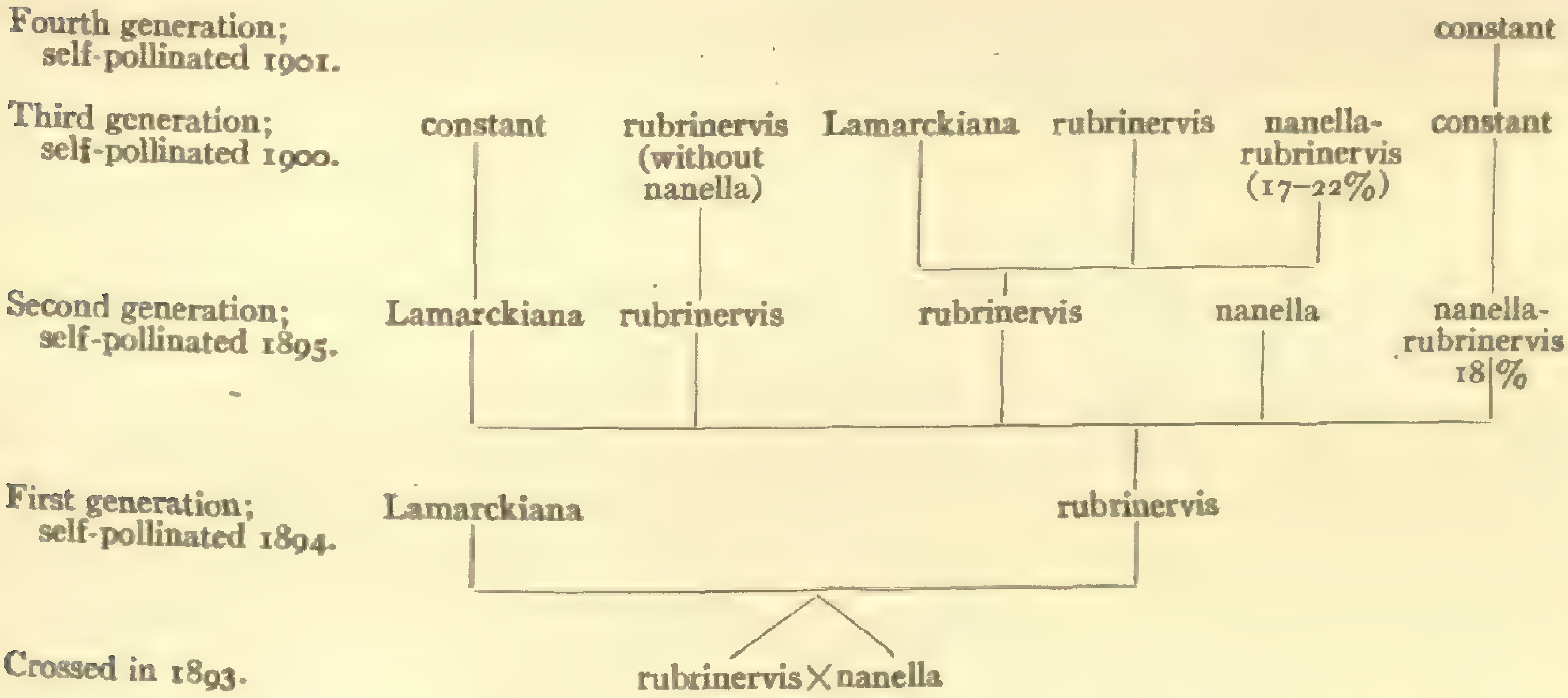
[3] I would suggest this term as an English equivalent for the German *Erbzahl* and shall use it in this sense in the rest of the paper.

The proportions of the parents appearing in a cross also fluctuate from other causes. In crossing *O. Lamarckiana* with *O. nanella* pollen, in one experiment when 90–100 seedlings were produced from one ovary the proportion of *O. nanella* was 44 per cent., but when the number of seedlings produced from an ovary was only 20–40, the proportion of *O. nanella* was reduced to 10 per cent. The quantity of pollen used in a cross also influences the offspring, and the proportions may be varied by experimental methods. Thus in one experiment (DEVRIES *l. c.* **2**:417), all of the 4–8 lobes of the stigma of *O. Lamarckiana* flowers were removed except one lobe or a small portion of one. They were then rather sparingly pollinated with *O. nanella* pollen (one flower being used to pollinate several), and of 1593 seedlings produced from 8 *O. Lamarckiana* plants whose flowers were thus treated, all were *O. Lamarckiana.* In another experiment all of the stigma was removed but one lobe, and of 1687 seedlings obtained only about 2 per cent. were *O. nanella.* Other experimental means of varying the results of a cross need not be mentioned here. But that such results can be obtained is of the greatest interest and suggests a line of inquiry as to the nature of the factors determining what forms will appear in a cross. This may also have a bearing on the determination of the chromosome number, though just what the connection may be cannot be guessed at present.

When two mutants are crossed the results show a much greater variation in numbers and forms. In some cases four types are produced in the F_1, though one or more of these types may be absent in any cross. *O. lata*×*O. nanella* may be taken as an example. In one experiment[4] the F_1 showed: *O. lata* 30 per cent., *O. Lamarckiana* 18 per cent., *O. nanella* 47 per cent., *O. nanella-lata* 5(?) per cent. The constant intermediate hybrid type *O. nanella-lata* is usually absent from this cross, and the percentage of the other types may vary widely. The *O. Lamarckiana* and *O. nanella* hybrids from this cross breed true, as does also *O. nanella-lata* when present. Since *O. lata* does not mature its pollen, its constancy cannot be tested by self-pollination.

One other instance of a cross between two mutants (*O. rubrinervis*×*O. nanella*) will be given, to show the complexity and variety of the results.


Fourth generation; self-pollinated 1901.
constant
Third generation; self-pollinated 1900.
constant
rubrinervis (without nanella)
Lamarckiana
rubrinervis
nanella-rubrinervis (17–22%)
constant
Second generation; self-pollinated 1895.
Lamarckiana
rubrinervis
rubrinervis
nanella
nanella-rubrinervis 18%
First generation; self-pollinated 1894.
Lamarckiana
rubrinervis
Crossed in 1893.
rubrinervis×nanella

In this case (DEVRIES *l. c.* **2**:451) *O. Lamarckiana* and *O. rubrinervis* were produced in the first hybrid generation, the latter on self-pollination producing (1) *O. Lamarckiana*, which was constant; (2) *O. rubrinervis*, part of which were pure and part split into *O. Lamarckiana*, *O. rubrinervis*, and *O. nanella-rubrinervis* as in the previous generation; (3) *O. nanella*, whose constancy was not tested; (4) *O. nanella-rubrinervis*, which bred constant through three generations. The form *O. nanella-rubrinervis* is an intermediate type between *O. rubrinervis* and *O. nanella;* it has never appeared as a mutation or in the first hybrid generation, but apparently arises only from self-fertilized hybrids of the second or later hybrid generations.

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[4] DEVRIES, HUGO, Ueber erbungleiche Kreuzungen. Ber. Deutsch. Bot. Gesells. **18**:435–443. 1900.

In these crosses it should be said that, while constancy of the forms appearing in the F_1 is the rule, exceptionally in one of the types which ordinarily breeds true an individual may appear whose progeny repeat the two types of the grandparents, thus showing a tendency to continue splitting (DEVRIES *l. c.* **2**:423).

SHULL'S[5] recent work on hybridization in the elementary species of Bursa (Capsella) shows that these produce ordinary Mendelian hybrids in no way comparable to Oenothera hybrids. In fact I think it is safe to say that no genus of plants or animals is known in which the conditions of hybridization are strictly comparable to those found in Oenothera. This peculiar type of hybridization is not confined to *O. Lamarckiana* and its mutants, but ordinarily appears when a mutant is crossed with another member of the genus, as *O. muricata*, *O. biennis*, *O. hirtella*, *O. suaveolens*, *O. hirsutissima*. In such cases the first hybrid generation usually contains both the parent forms in widely varying proportions, and these in the F_2 are found to breed true. Thus the same type of hybrid is produced as is usual when a mutant is crossed with *O. Lamarckiana*.

The phenomena of hybridization in Hieracium are more nearly like those of Oenothera than any other genus, so far as I know. MENDEL'S[6] original work, continued recently by OSTENFELD,[7] has given us a view of the hybridization conditions in this genus. MENDEL showed in a number of Hieracium crosses that the F_1 is heterogeneous, including some intermediate types and some very near to or indistinguishable from the parents. In the case of *H. praealtum* × *H. flagellare*, the F_2 obtained by self-pollinating the hybrids of the F_1 was shown to be the same as the F_1, all the forms of the latter breeding true. Ostenfeld[8] first showed the presence of apogamy in the genus by castration experiments. Murbeck[9] has since found that the egg in these cases develops the embryo parthenogenetically. The absence of fertilization in some cases is thus a factor at least in the peculiar form of hybridization. Ostenfeld[7] has recently extended these studies to a considerable number of species. Among other species he has shown by castration experiments, confirmed by the cytological investigations of Rosenberg,[10] that *H. excellens* is partly parthenogenetic and partly develops normally fertilized eggs; its pollen is also sterile. Rosenberg found in this form the interesting condition which he calls apospory, where a cell of the nucellus enlarges and obliterates the normally formed tetrad of megaspores. This cell completes the embryo sac morphology and the egg develops without fertilization. More rarely apogamous embryo sacs are formed, as in Taraxacum. Usually, however, normal tetrad formation, with reduction of chromosomes, takes place, followed by fertilization. Part of the plants produced in a cross are then pure *H. excellens* produced from apogamous or aposporous embryo sacs and part are real hybrids.

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[5] SHULL, G. H., Elementary species and hybrids in Bursa. Science **25**:590–591. 1907.

[6] MENDEL, G., Ueber einige aus künstlicher Befruchtung gewachsene Hieracium-Bastarde. Verh. Naturf.-Vereins. Brünn. **8**:26–31 (Abhandlungen). 1869.

[7] OSTENFELD, C. H., Castration and hybridization in the genus Hieracium. Rep. 3d Internat. Conf. on Genetics. Jour. Roy. Hort. Soc. London **24**:285–288. 1900.

———, Experimental and cytological studies in the Hieracia. I. Castration and hybridization experiments with some species of Hieracia. Bot. Tidssk. **27**:225–248. *pl. 1.* 1906.

The similarity of this form of hybrid to the *O. lata*×*O. Lamarckiana* cross suggests the presence of apogamy in *O. lata* also, though it is highly improbable that this can explain all the phenomena of hybridization concerned. In the latter cross only the two parent types are produced and the *O. Lamarckiana* breeds true, while in the Hieracium cross several types are produced intermediate between the parents, in addition to the pure *H. excellens*, but experiments of Ostenfeld have not yet been carried far enough to determine the character of later generations, and the number of plants he has obtained from seeds has been in some cases too small for entirely satisfactory results.

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[8] Ostenfeld, C. H., Zur Kenntnis der Apogamie in der Gattung Hieracium. Ber. Deutsch. Bot. Gesells. **22:**376–381. 1904.

———, Weitere Beiträge zur Kenntnis der Fruchtentwickelung bei der Gattung Hieracium. *Idem* 537–541.

[9] Murbeck, S., Parthenogenese bei den Gattungen Taraxacum und Hieracium. Bot. Notiser **1904:**285–296.

[10] Rosenberg, O., Ueber die Embryobildung in der Gattung Hieracium. Ber. Deustch. Bot. Gesells. **24:**157–161. *pl. 11.* 1906.

[10a] ———, Experimental and cytological studies in the Hieracia. II. Cytological studies on the apogamy in Hieracium. Bot. Tidssk. **28:** 143–170. *pls. 1–2.* 1907.

The Oenothera and Hieracium hybrids mentioned may be said to resemble each other in that in both the F_1 is heterogeneous, though the types of which the F_1 is composed differ in the two crosses, agreeing only in that one of the types in each is the pure mother parent. The abortive character of the pollen in *O. lata* may also be said to favor rather than otherwise the probability of apogamy in this species, as it is well known that apogamous species frequently do not mature their pollen. This suggestion of apogamy in *O. lata* will be examined in another light in connection with the discussion of the number of chromosomes.

MILLARDET'S[11] "false hybrids" in Fragaria and Rubus, in which only one of the parent types (usually the mother) is produced in the hybrid, and this breeds true, may possibly be regarded as extreme cases of the same type of hybrid as some of the Oenothera crosses.

HURST,[12] among a large number of crosses of orchids which showed many types of hybridization, found eleven crosses between different genera in which only one of the parent types was reproduced, this being in every case the mother (p. 104). Large numbers of the hybrids were grown in some cases. He concluded that in at least eight of these "false hybrids" self-pollination was impossible, and that the embryos probably developed apogamously, perhaps on account of the stimulus from the presence of foreign pollen tubes in the ovary, but without fertilization. Oenothera itself may produce hybrids of this type. Thus DEVRIES found that *O. Lamarckiana* ♀ ×*O. biennis* ♂ gives only *O. biennis* in the F_1 and F_2 (*l. c.* **2**:31). This cross made in the New York Botanical Gardens, however, gave in addition to several *O. Lamarckiana* plants, which MACDOUGAL[13] thinks probably came from foreign *Lamarckiana* pollen, four types, none of which were the same as either parent. Thus entirely different results may be obtained under different conditions.

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[11] MILLARDET, M. A., Note sur l'hybridation sans croissement ou fausse hybridation. Mem. Soc. Sci. Phys. et Nat. Bordeaux IV. **4**:347–372. 1894.

[12] HURST, C. C., Notes on some experiments in hybridization and cross-breeding. Jour. Roy. Hort. Soc. London **24**:90–126. *figs. 9–41.* 1900.

[13] MACDOUGAL, D. T., Mutants and hybrids of the Oenotheras. Publ. 24, Carnegie Institution, Washington, pp. 56. *pls. 22.* 1905.

The possibilities of apogamy in other mutants are apparently not so good, and such a condition seems rather unlikely, especially in *O. nanella*, where some of the hybridization results practically exclude the possibility of apogamy in these cases. Thus, *O. nanella* ♀ × *O. biennis* ♂ gave (DEVRIES *l. c.* **2**:476) in two crosses 554 plants, none of which were *O. nanella;* while the reciprocal cross gave 96–100 per cent. *O. nanella* among 356 plants. Hence in both cases the pollen parent was practically the only form appearing in the F_1, so that apogamous embryos, at least of any kind known at present, could not have been formed.

THE NUMBERS OF CHROMOSOMES

In my earlier paper[1] it was shown that the sporophyte number of chromosomes in *O. lata* is fourteen, while in the *O. Lamarckiana* plants appearing in the first hybrid generation from a cross with *O. lata*[14] the number is at least twenty. It was assumed therefore that the pure *O. Lamarckiana* parent had at least twenty chromosomes as the sporophyte number. Examination has shown, however, that in the pure *O. Lamarckiana* the sporophyte number is fourteen. This creates a remarkable and unexpected situation, which may be illustrated thus:

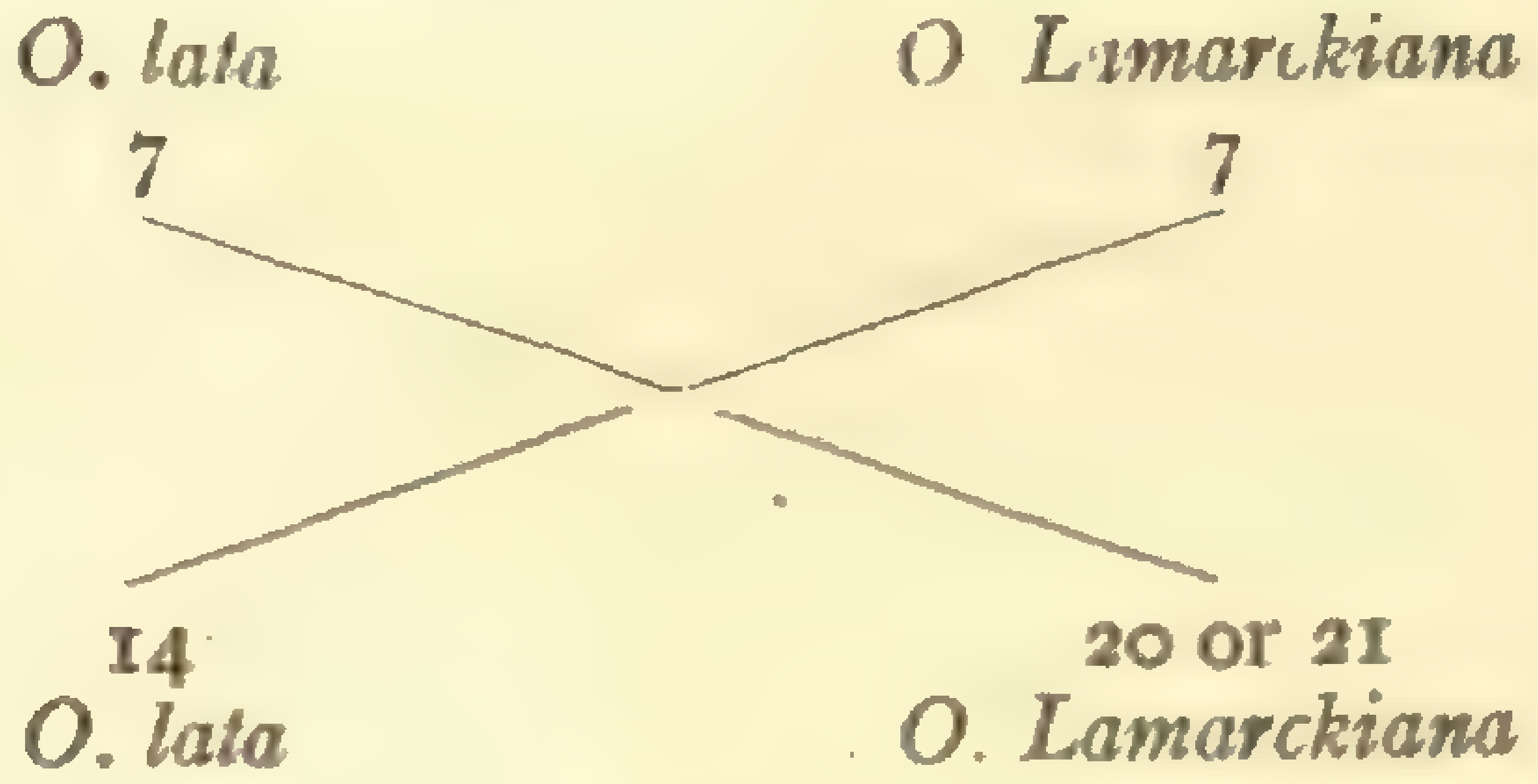

FIG. 3

Two plants, whose gametophyte number of chromosomes is seven, when crossed give rise in the first hybrid generation to the two parent forms, one of which has fourteen chromosomes as the sporophyte number, while the other has twenty or twenty-one.

In *O. lata* the count of chromosomes was made in the pollen mother cells and found to be fourteen. It has since been made in various somatic tissues of the flower, and is found to be constantly fourteen so far as observed. There has been no indication whatever that the number is ever higher. In the *Lamarckiana* hybrid it has been found from a number of counts in the floral tissues that the number of chromosomes in the somatic tissues is twenty or twenty-one, and I have found no reason to think it varies. In the pollen mother cells the number of chromosomes in the metaphase and anaphase of the heterotypic mitosis is usually twenty or twenty-one. Occasionally the number in early anaphase appears to be less, but this may be due to a tardy separation of some of the paired chromosomes in the equatorial plate; further study is required to determine this point. A large number of telophases of this mitosis were counted which showed ten chromosomes each. In one case there appeared to be eleven chromosomes in a telophase, though the greater majority at least show ten in each daughter nucleus. Occasionally a chromosome lags behind in the equator of the spindle until late anaphase, and this may make the number twenty-one. Such a case is figured in my former paper (*pl. 4*, *fig. 39*). This is not always the case, however, as shown by *fig. 38*, in which there are ten chromosomes in each daughter nucleus, but none left behind in the equator of the spindle. It is possible that a single unpaired chromosome might be present in metaphase and be lost in the cytoplasm as the paired chromosomes separated and went to the poles. It is certain that in many pollen mother cells ten chromosomes go into each daughter nucleus in the heterotypic mitosis. Whether the number in the somatic tissues is twenty or twenty-one has not been determined with certainty, as it is a matter of very considerable difficulty. The further discussion will reveal the reason for suggesting that the sporophyte number of chromosomes in the *Lamarckiana* hybrid is twenty-one rather than twenty.

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[14] For the sake of brevity I shall refer to the *O. Lamarckiana* plants appearing from flowers of *O. lata* pollinated by *O. Lamarckiana* as "the *Lamarckiana* hybrid."

O. Lamarckiana, the parent, has fourteen chromosomes as the sporophyte number, so far as the plants have been examined. This count was made constantly in the floral tissues. The homotypic mitosis in the pollen mother cell shows seven chromosomes constantly so far as observed, a large number of counts being made in various stages of this mitosis. It is doubtless true that chromosome counts as ordinarily made come from a very few individuals. In the case of the *Lamarckiana* hybrid I have examined material from two individuals and from different flowers in each; these plants were grown in different seasons. In every count the number of chromosomes in the somatic tissues has been twenty or twenty-one, though I have been as yet unable to determine with certainty between these two numbers. Any cytologist is acquainted with the fact that one region of a chromosome group is likely to be obscure enough, owing to close aggregation of the chromosomes, to prevent absolute certainty in making a count of the exact number, unless the number of chromosomes happens to be a small one. The evidence already mentioned shows beyond a doubt that, in the large majority of cases at least, ten chromosomes enter each daughter nucleus in the heterotypic mitosis, though it may be that there are occasionally eleven chromosomes in one of the daughter nuclei.

Several plants of *O. lata* and the pure *O. Lamarckiana* have been examined, all having fourteen chromosomes, which makes it probable that fourteen is the number found in all the pure individuals of these species, and twenty or twenty-one the number found in all the individuals of the *Lamarckiana* hybrid. But it will be necessary to determine the count in several more plants of each of these races before this point can be settled with certainty.

It will be of interest to know whether the number of chromosomes in the *Lamarckiana* hybrid remains constant in later generations, and also what happens when the *Lamarckiana* hybrid having twenty or twenty-one chromosomes is crossed with *O. lata* or with pure *O. Lamarckiana* having fourteen chromosomes. I am now growing plants from crosses made in last season's cultures, which it is hoped will determine these interesting points.

THE HETEROCHROMOSOMES

In my former paper[1] (p. 91), large rings of chromatin were described as sometimes occurring in the pollen mother cells of *O. lata*, cut off from the spirem after synapsis. In the heterotypic mitosis in *O. lata* and the *Lamarckiana* hybrid small bodies are found, ring-shaped (or hollow) but of the same size as the chromosomes, from which they are otherwise indistinguishable. These may be on the spindle or in the cytoplasm, as described in that paper. It was believed that the smaller ring-shaped chromatic bodies were condensed from the larger rings found in the spirem stage. It is possible, however, that the latter are merely irregularities occurring during pollen degeneration in *O. lata*, for it is well known that a variety of irregularities, in addition to the ones described, may occur in synapsis and the reduction mitosis in sterile hybrids. This leaves unexplained the origin of these bodies called heterochromosomes. On the other hand, the evidence from staining properties and from other considerations, as given in the paper referred to, is against their origin from nucleoli. The same bodies have since been found in the reduction mitoses in *O. Lamarckiana*, where they persist, in some cases at least, through both mitoses to the formation of pollen tetrads. For the present, therefore, the origin and possible significance of these bodies may be considered to be a matter of doubt, in regard to which no conclusions can be drawn until further evidence is obtained.

POSSIBLE EXPLANATION OF THE CHROMOSOME NUMBERS

A number of possible explanations of the origin of the chromosome number in the *Lamarckiana* hybrid will at once occur to botanists. It must be said, however, that all of them appear unlikely, and no explanation can be given on the basis of our present knowledge in regard to chromosome numbers. It is to be expected that further investigation will disclose the sources of the extra chromosomes in the *Lamarckiana* hybrid, but for the present some possibilities may be suggested.

It would seem more probable, because more in accord with present views of chromosomes, that the sporophyte number of chromosomes in the *Lamarckiana* hybrid arises at the time of fertilization by the union of nuclei the sum of whose chromosomes is twenty-one, than that it arose through the subsequent divisions of certain chromosomes. The experimental results of NĚMEC[15] and others, in which somatic nuclei are made to fuse and subsequently divide, showing mitotic figures with chromosomes whose number is the sum of the number of chromosomes in the nuclei that entered the original fusion, indicate the persistency of individual chromosomes in such cases. Such results increase the probability that the number of chromosomes found in the somatic tissues of an individual arose with the genesis of the individual and has persisted in all subsequent cell generations. Of course there is the possibility that a higher number of chromosomes might originate through the longitudinal division or the fragmentation of certain chromosomes; but no constant size-differences have been found among the chromosomes of any of the forms or between the chromosomes of the different races examined.

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[15] NĚMEC, B., Ueber die Bedeutung der Chromosomenzahl. Bull. Internat. Akad. Sci. Bohême **10**:1–4. 1906.

There are a number of ways in which it would be possible for fusion nuclei having twenty-one chromosomes to be formed during the period of fertilization, since the gametophyte number of chromosomes is seven.

(1) It is possible that *O. Lamarckiana* might produce two kinds of pollen, having respectively seven and fourteen chromosomes. My examination of the conditions of pollen development in *O. Lamarckiana* has thus far revealed no evidence whatever in favor of such an hypothesis. Apparently all the pollen mother cells undergo the reduction divisions, in which the number of chromosomes is reduced from fourteen to seven in the usual way.

(2) It is possible that *O. lata* might produce two kinds of eggs, having respectively seven and fourteen chromosomes. If both these kinds of eggs were fertilized with *O. Lamarckiana* pollen and produced embryos, we should have plants resulting with fourteen and twenty-one chromosomes. The difficulty here, however, is that on such an hypothesis the union of seven *lata* chromosomes with seven *Lamarckiana* chromosomes would produce a *lata* plant; while the union of fourteen *lata* chromosomes with only seven *Lamarckiana* chromosomes would produce a *Lamarckiana* plant, a situation which is highly improbable, to say the least.

(3) Another possibility is that all the eggs of *O. lata* have the unreduced number of chromosomes, and that part of them develop without fertilization (parthenogenetically), producing *O. lata* plants with fourteen chromosomes; while others are fertilized with *O. Lamarckiana* pollen, and produce *Lamarckiana* plants having twenty-one chromosomes (*fig.* 3). This assumption is perhaps as reasonable as any, but no case is known of an unreduced egg being fertilized.

(4) Another possible source of twenty-one chromosomes is by the union of both male cells with the egg in fertilization. This, though very unlikely, is at least a theoretical possibility.

(5) It is conceivable that the triple fusion nucleus in double fertilization, instead of the egg, might form the embryo. The only known case of the endosperm developing anything resembling an embryo is Balanophora. TREUB[16] studied *B. elongata* and the same conditions were afterward found in *B. globosa* by LOTSY.[17] Fertilization does not take place in these forms, and the egg and synergids soon degenerate, while the upper endosperm nucleus enlarges and divides, forming a mass of endosperm tissue. In the midst of the endosperm a group of smaller cells is cut off, forming a "pseudembryo," which was followed to the five or ten cell-stage. Tetrad formation apparently does not take place, so that there is probably no reduction of chromosomes, the "pseudembryo" having the $2x$ number.

All of these possibilities, therefore, are without parallel in our present knowledge, but it seems most probable that the source of the twenty-one chromosomes is to be sought in some such situation during fertilization, or the genesis of the individual having this number of chromosomes. It is hoped that further investigation of megaspore and embryo sac development and fertilization in *O. lata* will lead to the explanation of this remarkable situation, though of course the real explanation may be quite different from any of the possibilities here suggested.

On any of these assumptions the number of chromosomes is twenty-one. If it is twenty, however, another explanation must be sought. The correctness of the latter number is supported by the fact that I have counted many telophases of the heterotypic mitosis, in which the number of chromosomes was ten in each daughter nucleus. Also if twenty-one chromosomes originated from the fusion of three nuclei, two of which represented one parent and one the other parent, it might be expected that in synapsis and the reduction mitosis a segregation of the chromosomes would indicate this origin. One might perhaps expect a pairing of seven chromosomes (maternal) with seven others (paternal), leaving the other seven unpaired to pass to either pole or remain out in the cytoplasm. ROSENBERG[18] found such a situation in the Drosera hybrid, where the ten chromosomes from one parent paired with ten of the twenty from the other parent, while the remaining ten chromosomes of the latter remained unpaired and were irregularly distributed or lost in the cytoplasm. But nothing of this kind has thus far been observed in the reduction divisions of the *Lamarckiana* hybrid, and instead ten chromosomes are apparently regularly distributed to each daughter nucleus in the heterotypic mitosis. It is pretty evident that the exact number of chromosomes cannot be satisfactorily settled until their origin is ascertained.

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[16] TREUB, M., L'organe femelle et l'apogamie du *Balanophora elongata* Bl. Ann. Jard. Bot. Buitenzorg **15**:1–22. *pls. 1–8.* 1898.

[17] LOTSY, J. P., *Balanophora globosa* Jungh. Eine wenigstens örtlich-verwittwete Pflanze. Ann. Jard. Bot. Buitenzorg II. **1**:174–186. *pls. 26–29.* 1899.

Not the least remarkable part of this situation is found in the fact that here we have two plants, the pure *O. Lamarckiana* and the *Lamarckiana* hybrid, which cannot be distinguished by their external characters, and yet differ widely in the number of their chromosomes. This difference in number assumes a different aspect, however, if we find, as seems most probable, that we have here merely an extra set of chromosomes from one parent. Such a situation need not necessarily interfere with the present views of persistency of chromosome numbers or even of the ordinary constancy in number for a species. A knowledge of the fate of these chromosomes in subsequent generations and crosses will probably aid largely in determining the general bearing of these facts on present views of the individuality and constancy in number of chromosomes.

It is suggestive that in the *Lamarckiana* hybrid, as ROSENBERG[10a] has found in the apogamous species of Hieracium, the number of chromosomes is much higher than in other species of the genus examined. In the apogamous species in various genera investigated in recent years, where the chromosome numbers are known, the number of chromosomes in apogamous species is nearly or exactly double the sporophyte number in closely related, normally fertilized members of the same genus. A list of these cases need not be given. There may be a suggestion here as to how variation in the chromosome numbers of a genus originates. The same author[19] finds that

[18] ROSENBERG, O., Ueber die Tetradentheilung eines Drosera-Bastardes. Ber. Deutsch. Bot. Gesells. **22**:47–53. *pl. 4.* 1904.

[19] ROSENBERG, O., Cytological investigations in plant hybrids. Rep. 3d Internat. Conf. on Genetics. Jour. Roy. Hort. Soc. London **24**:289–291. 1906.

in *H. excellens* the egg cells have different numbers of chromosomes, owing to irregularities in the reduction divisions. When this form is crossed with another species, the hybrids of the F_1 have different numbers of chromosomes. Whether this is the cause of the different types in the F_1 is not ascertained.

It seems probable, or at least possible, that there is a connection between the type of hybridization in Oenothera and the chromosome numbers, though just what that connection may be is at present quite unknown. Apparently whatever determines the twenty or twenty-one chromosomes determines also that the parent shall have the *O. Lamarckiana* characters. There is thus a possibility that this may be found to have a bearing upon the cause of dominance and recessivity in Mendelian hybrids, the characters of the individual being determined in this case by the presence or absence of the extra chromosomes. CANNON'S[20] suggestion that the Mendelian segregation of characters results from the segregation of maternal and paternal chromosomes in the reduction mitoses is as yet a hypothesis without proof, though ROSENBERG'S[21] recent paper, in which he states that in the pollen development of the Drosera hybrid occasionally two pollen grains of the tetrad have the morphology of one parent and two that of the other, shows that in some cases, at least, segregation of characters takes place at this point in the life history.

Practically the same theory of the segregation of the characters and purity of the germ cells in plant hybrids on the basis of the chromosomes (idants) was put forward by WEISMANN[22] in 1892, in connection with his theory of the germ-plasm. At this time the Mendelian hybrids had not been rediscovered, and complete segregation of the characters of the parental types was regarded as a rare occurrence in hybrids. It may be worth while to quote WEISMANN'S statement (p. 299):

> The germ-mother cells of the hybrid contain a group of idants (chromosomes) derived from the paternal, and another from the maternal ancestral species. If therefore the "reducing-division" halves the germ-plasm of these mother-cells in

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[20] CANNON, W. A., A cytological basis for the Mendelian laws. Bull. Torr. Bot. Club **29**:657–661. *fig. 1.* 1902.

[21] ROSENBERG, O., Erblichkeitsgesetze und Chromosomen. Botaniska Studier, Upsala, pp. 237–243. *figs. 5.* 1906.

[22] WEISMANN, AUGUST, The germ-plasm. English translation. New York. 1898.

such a manner that idants of the mother alone reach one ripe germ-cell, and those of the father alone are contained in another, it is possible that two such germ-cells may unite when fertilization takes place between these hybrids. In such a case a plant completely resembling one of the ancestral forms would arise, for it would have been produced from a germ-plasm which contains idants of this species only.

He concludes, however, (on a theoretical basis only) that this rarely happens.

To obtain the Mendelian ratios in hybrids on the basis of the purity of the germ-cells, it is necessary to assume that the mechanism of the reduction mitoses regularly segregates the maternal and paternal chromosomes, and that their distribution to the daughter cells in such cases is not merely a matter of chance, or that a part merely of the chromosomes from one parent can determine the dominance of that form. ROSENBERG[23] has elaborated such a scheme of chromosome segregation in connection with his study of *Drosera rotundifolia* × *D. longifolia*. He found that in the metaphase of the heterotypic mitosis in the pollen mother cell the chromosomes of the two parents, which can be distinguished by their size, are not all oriented, with for example the paternal chromosomes toward one pole of the spindle in the equatorial plate, but some from each parent will enter both daughter nuclei, their orientation on the spindle being thus determined by chance. The Drosera hybrid does not show complete dominance, but is intermediate, some of the characters being nearer to either parent. The character of the hybrid in later generations has not yet been determined.

DEVRIES'[24] conception of the segregation in Mendelian hybrids is that where the parents differ in one unit character this character will be represented in the hybrid by a single *Anlage* from each parent. If these *Anlagen* are assumed to be each represented by a single chromosome, the corresponding members of the other chromosome pairs being qualitatively alike, this would give, as ROSENBERG[23] points out, a chromosome basis for Mendelian segregation of characters. In the formation of the megaspores and microspores, half would contain the chromosome representing the peculiar paternal character, and half the chromosome representing the maternal. The germ-cells would thus all be pure in regard to this character, and in self-fertilization of the hybrid, according to the laws of chance the usual percentages of a Mendelian hybrid would arise.

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[23] ROSENBERG, O., Ueber Reduktionstheilung in Drosera. Meddel. Bot. Inst. Stockholm, pp. 13. *figs. 20.* 1904.

[24] DEVRIES, HUGO, Befruchtung und Bastardierung. Leipzig. pp. 62. 1903.

OTHER CYTOLOGICAL OBSERVATIONS

Several interesting cytological observations, a detailed description of which will be presented at a later time, may be briefly stated here. In the heterotypic mitosis in the pollen mother cells of the *Lamarckiana* hybrid, the usual split in the chromosomes, in the anaphases, which is generally described as a premature split for the homotypic mitosis and is believed by many cytologists to be the reappearance of a split which occurred at the time of synapsis, occurs as described in my former paper. In the early telophases, before there is any indication of a nuclear membrane around the daughter nuclei or of the beginning of a passage into the semi-resting condition, which occurs later, chromosomes having the appearance of distinct tetrads are frequently found. The indications are that this tetrad appearance, which is often very clear and characteristic, may be due to the two halves of a daughter chromosome (which were formed by the split in the anaphases of the heterotypic) remaining side by side and each becoming clubbed at the ends, the portion between these ends in each remaining only as a very delicate connecting thread. This gives the appearance of four spherical bodies of approximately equal size, connected in pairs in one direction by two parallel delicate threads. In other cases the tetrads have quite a different shape, having rather the appearance of a hollow ring drawn out sharply at the four corners. In still other cases, in this telophase, chromosomes are seen having the shape of a pair of spheres close together, or a dumb-bell, and often chromosomes are found at this stage showing no indication of even a double nature, but appearing univalent. This variation in form does not obscure the distinctness of the chromosomes, which are usually clearly distinguishable from each other at this time, and easily counted. All these different forms may be found together in the same nucleus, though so far as observed one form usually predominates in a given telophase. Figures showing these appearances will be published later.

In the homotypic mitosis, as observed in *O. Lamarckiana*, the chromosomes usually become two-lobed in the anaphases. Just how this shape arises from the pear-shaped chromosomes of the early anaphase has not been determined. In the telophase of this mitosis the chromosomes are nearly always two-lobed or dumb-bell-shaped and can be readily counted (seven in *O. Lamarckiana*) in this condition. They soon become more or less irregular in outline, however, as the nuclei pass into the resting condition, but this characteristic shape usually persists for a short time at least after the formation of the nuclear membrane.

Several interesting features have appeared in connection with the examination of nuclear divisions, in various somatic tissues, a work which is not yet completed. All the tissues examined are flower tissues about the time when the reduction divisions are taking place in the pollen mother cells or later. The conditions so far as observed are identical in corresponding tissues of the three forms examined (*O. lata*, *O. Lamarckiana*, and the *Lamarckiana* hybrid), except for the difference in the number of chromosomes. In the tissue of the anther wall and in the rapidly dividing tissues of the young petals, in both of which a great many chromosome counts were made, the chromosomes are crescents, rods, or loops in metaphase and the early anaphases, the apices of the loops converging in telophase to the poles of the spindle. In the telophase these chromosomes also become two-lobed or dúmb-bell-shaped. This shape is very characteristic and apparently constant, or at least occurs very generally at this stage. Observations which are as yet incomplete indicate that in the early telophase these chromosomes begin to appear two-lobed. This shape is very clear a little later, about the time the membrane of the daughter nucleus is formed. The chromosomes can be distinctly counted at this time, and the number is apparently constant in each form. It seems probable that this clubbing of the ends of the chromosomes to form dumb-bells or two-lobed chromosomes in the telophase of the mitoses in these tissues is the same thing that happens in the telophase of the heterotypic mitosis, giving rise to the tetrad appearance, and in the telophase of the homotypic, giving rise to the two-lobed or dumb-bell-shaped chromosomes. Whether this lobing of the chromosomes giving a bivalent appearance is in all these cases a preparation for the split in the next mitosis cannot at present be determined. The paucity of investigations on the somatic mitoses in plants leaves open the possibility that some of the phenomena of the reduction mitosis to which a special significance has been attached may find their counterpart in ordinary somatic mitoses. It is believed that further study will settle the interpretation of these appearances.

Measurements have shown that the size of the cells, nuclei, and chromosomes in the anther wall is on the average approximately the same as in the petals, though there is considerable variation in the size of the cells of the latter. It is interesting to note that while the chromosomes in the somatic tissues are loops in the metaphase and early anaphases, in the pollen mother cells the chromosomes are usually spherical or pear-shaped in these stages of both the reduction mitoses. This difference is very striking. In the telophase of the homotypic, however, the characteristic shape is apparently the same as in the corresponding stage of somatic mitoses, that is, two-lobed. Measurements indicate that the somatic chromosomes are at this stage considerably smaller than the homotypic chromosomes, though there appears to be much variation in the size of the former.

SUMMARY

1. In my previous paper the sporophyte number of chromosomes in *O. lata* was found to be fourteen, and in the *Lamarckiana* hybrid obtained by crossing *O. lata* with *O. Lamarckiana* pollen, at least twenty. The number of chromosomes is now found to be twenty or twenty-one constantly in all the plants of the *Lamarckiana* hybrid examined, while the number in the pure *O. Lamarckiana*,[25] as well as in *O. lata*, is fourteen, the reduced number being seven. These results are obtained from a large number of counts in various stages of the reduction mitoses and also in the somatic divisions (floral tissues). Thus the pure *O. Lamarckiana* and the *Lamarckiana* hybrid, which are identical in external appearance, differ widely in the number of their chromosomes.

2. The origin of the bodies called heterochromosomes, which are present in the reduction divisions in all the forms studied, is a matter of

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[25] J. M. GEERTS, in a short paper just received (Ueber die Zahl der Chromosomen von *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. **25**:191–5. *pl. 6*. 1907), also finds that the sporophyte number of chromosomes in the pure *O. Lamarckiana* is 14 and the gametophyte number 7.

doubt, and until their mode of origin is ascertained no significance can be attached to them.

3. In the telophase of the heterotypic mitosis in the pollen mother cells of the *Lamarckiana* hybrid, the chromosomes frequently have distinctly the form of tetrads. In the homotypic mitosis of *O. Lamarckiana*, as well as in the somatic mitoses (in various floral tissues) in all forms studied, the chromosomes are two-lobed in the telophase. The tetrad appearance is probably due to the same lobing of the bivalent chromosomes that takes place in the telophase of the homotypic and somatic mitoses.

This investigation has been carried on under the supervision of Professor John M. Coulter and Dr. Charles J. Chamberlain.

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MORPHOLOGICAL AND ANATOMICAL STUDIES OF THE VEGETATIVE ORGANS OF RHEXIA

THEO. HOLM

(WITH PLATES I AND II)

An anatomical classification of the Melastomaceae has been proposed by VAN TIEGHEM,[1] who divides the family into two tribes: Melastomeae and Memecyleae. In the former the secondary hadrome shows the normal structure, while in the latter the secondary hadrome incloses groups of leptome in as many concentric bands as the stem shows annual rings. The Melastomeae comprise four subtribes: Dermomyelodesmeae, with supernumerary mestome strands in the cortex and pith; Dermodesmeae, with supernumerary mestome strands in the cortex alone; Myelodesmeae, with supernumerary mestome strands in the pith alone; and Adesmeae, without supernumerary mestome strands. The Memecyleae comprise two subtribes: Pternandreae, without sclereids in the leaves; and Mouririeae, with sclereids in the leaves. The genus Rhexia belongs to the Dermomyelodesmeae.

Among other anatomical works may be mentioned those by PFLAUM,[2] PALÉZIEUX,[3] and VÖCHTING,[4] and also a very detailed diagnosis of the family in SOLEREDER'S *Systematische Anatomie der Dicotyledonen* (p. 405).

It would thus appear as if the family had already been treated to such an extent that little if anything of real importance could be added, a fact fully appreciated by the author. However, the study of internal structure is not always accompanied by a corresponding treatment of the external, and so far the Melastomaceae have not yet been thoroughly investigated. The monograph contributed by COGNIAUX[5] is purely systematic and adds nothing to the natural history of these interesting plants. Copious as is the literature, very little attention has been paid to the following questions: how the plants grow, how they develop from seeds to mature plants, and how well the structural characteristics are preserved under various conditions.

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[1] Classification anatomique des Melastomacées. Bull. Soc. Bot. France **38**: 114. 1891.

[2] Anatom.-systemat. Untersuch. d. Blattes der Melastomaceen. Diss. München, 1897.

[3] Anatom.-systemat. Untersuch. d. Blattes der Melastomaceen. Bull. Herb. Boiss. **7**: appendix v. 1899.

[4] Der Bau und die Entwickelung des Stammes der Melastomaceen. Hanstein's Bot. Abhdl. **3**: 1. 1878.

Although the family is most widely distributed in America, very few species occur north of the tropics, and Rhexia is the only genus that occurs in the United States and Canada, with about ten species. Two of these, *R. virginica* and *R. mariana*, occur in the District of Columbia, the former extending as far north as Ontario, the latter to New Jersey. They both inhabit sandy swamps, associated with *Lilium superbum*, certain Cyperaceae (Scleria, Fimbristylis, Scirpus, and Carex), Polygalaceae, Violaceae, etc.

Having had the opportunity of studying these two species in the field at various seasons, I have found several points in their external structure which have not hitherto been described, and which may serve as a small contribution to the knowledge of the life-history of these interesting plants. To this is added a brief anatomical description of the vegetative organs, and especially of the roots, since these have not been studied heretofore.

Rhexia virginica L.

While studying the vegetative propagation exhibited by representatives of the local flora, I never was able to find any specimen of this species with a rhizome as described in the various manuals. According to BRITTON, GRAY, and SMALL, this species should possess "horizontal, slender, and tuberiferous rootstocks." That this statement is very incorrect may be seen from the following notes, in which I shall endeavor to show that the underground organs described as tuberiferous rootstocks are simply tuberous roots; and that the development of root-shoots is of great importance to the plant, being its only means of vegetative propagation.

Root-shoots of adult specimens, like those of *figs. 3* and *4*, do not give any clear idea of the remarkable way in which this herbaceous plant persists. In *fig. 3* a root-shoot is represented which at first glance may suggest a "slender tuberiferous rootstock" with a basal stem-portion, subterranean and covered with scale-like leaves. In *fig. 4*, however, a larger tuberous body is seen, from which several stems have developed, whose irregular position does not indicate that they have arisen from the axils of opposite leaves. As a matter of fact, there are neither leaves nor leaf scars to be observed upon this tuberous organ. The "rhizome" represented in *fig. 4* is the one most frequently found in flowering or fruiting specimens. A closer examination shows that the tuberous organs are not tubers, but tuberous roots. Moreover, in *fig. 3* the small tuberous body is borne upon a slender branch, which is seen to be a secondary root and not a stolon, since it bears no leaves. If these organs were stems, they would have been provided with opposite leaves like those of the aerial shoots, and the shoots would necessarily have occupied a much more definite position than those shown in *fig. 4*. Moreover, the internal structure of these organs proved to be that of a true root. This is the only type of "rhizome" that I have found in the very many flowering and fruiting specimens examined.

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[5] DeCandolle's Monogr. phanérog. 7:385. 1891.

The development of root-shoots is a phenomenon very frequently observed in our herbaceous and woody plants, but thus far we know a very limited number of plants that persist only as root-shoots. It was very desirable, therefore, to study the younger stages and especially the seedlings of Rhexia. On account of their diminutive size they are difficult to find in nature, since they are always more or less hidden by the rank vegetation that covers the swamps. However, I succeeded in detecting some small patches of young plants among which there were many seedlings. One of these is shown in *fig. 1*, which represents the complete root system, the very small epigeic cotyledons (*Cot*), and the basal internodes of the aerial shoot. At this stage the primary root (*R*) is the main root of the young shoot; it bears several lateral and very thin branches, two of which are opposite and developed beneath the cotyledons. These two roots commence to swell, and during the summer they show a local thickening in the shape of a fusiform tuber (*r*). A few secondary roots sometimes develop from the first internode a short distance above the cotyledons. At the end of the first season the shoot dies down to the ground, and the primary root withers with the exception of the two lateral swollen branches, which winter over as two separate roots.

In the following spring a young shoot develops, with scale-like, opposite leaves at the basal nodes, and with several pairs of secondary roots from the nodes, while a dark-colored tuberous body occurs at the base of the shoot. One or more of the secondary roots soon commence to increase in thickness, forming fusiform tubers like the one described above on the root of the seedling. *Fig. 2* shows a root-shoot; the short, dark tuber at the base of the shoot represents the lateral tuber of the seedling (*r* in *fig. 1*), and the shoot is developed not from the base of the tuber but from its upper face. If the shoot had continued the axis of the swollen root, there would have been a persistent primary root, but such a case was not observed; the shoot invariably occupied the position shown on the root marked *r* in *fig. 2*, where a bud is seen near the base on the upper face of the tuber. This bud is to develop a new and independent plant during the next year.

The specimen thus described (*fig. 2*) represents the root-shoot of the seedling and lives only one year, the persisting part belonging to a secondary root. Older specimens, like those in *figs. 3* and *4*, show the same course of development, but the shoots are more vigorous and the tuberous roots much larger. The secondary roots develop in pairs from the nodes, between the opposite scale-like leaves. These roots are quite long, branch freely, and are able to produce shoots as described above. Although the underground portion of the stem bears several leaves, none of these were found to subtend buds, and the shoot dies down completely at the end of the season. The tuberous roots, on the other hand, may live for three years, if not longer; the large specimen represented in *fig. 4* was fully three years old. When these root-tubers persist for more than two years they develop several shoots (*fig. 4*), and several strong, amply branching, lateral roots.

An over-wintering stage is shown in *fig. 5*. The tuber occupies here a horizontal position, and the shoots for the next year are already visible as buds on small stems with scale-like leaves and quite distinct internodes; the place of development of these minute shoots is along the upper face of the root. It is only when the tuber occupies a more or less vertical position that the shoots show a tendency to push out from near the apex, as may be seen in *fig. 3*.

Rhexia virginica, therefore, exhibits a very singular type of vegetative propagation, that is, one restricted entirely to the development of root-shoots.

THE INTERNAL STRUCTURE OF THE VEGETATIVE ORGANS

The roots

The secondary and lateral roots and the slender portions (apical and basal) of the tuberous roots have the same structure, modified only by age. In the tubers, on the other hand, there is a very different structure, since they remain active for a longer time and are the seat of a continuous development of aerial shoots, vegetative or floral. In the capillary lateral roots the primitive root structure remains unchanged, since they persist only one season. In the slender secondary and stronger lateral roots, which develop from the tuberous portion, the structure becomes changed at an early stage on account of the development of cambial strata from the conjunctive tissue on the inner face of the leptome strands, resulting in an increase in thickness of the stele and a gradual obliteration of the primitive structure. These roots may persist and remain active, therefore, for a longer time than do the capillary roots. However, the increase in thickness of the stele does not always cause a rupture of the surrounding tissues, accompanied by secondary formation (cork and secondary cortex); the endodermis, cortex, exodermis, and epidermis often remain entire for some time. As soon as the development of cork commences (in Rhexia from the pericambium), the peripheral tissue necessarily becomes broken, though without being thrown off.

A much greater increase in thickness is seen, of course, in the tuberous roots. In them, even during the very first period of their growth, the activity of the pericambium is so rapid that the peripheral tissues from endodermis to epidermis are thrown off completely, and are replaced by strata of cork and secondary cortex originating from the pericambium. Hence the structure of the tuberous roots shows a marked deviation from that of the other roots. In *fig. 10* there are shown the several layers of cork (*P*), the broad parenchyma of secondary cortex (*C*), and a continuous circle of cambium strata surrounding a broad cylinder of thin-walled parenchyma in which the long but very narrow rays of mestome radiate from the primitive root-stele.

The number of mestome strands varies in accordance with the thickness of the tuber; the largest number observed was ten, representing the growth of one season.

The minor structure of these various tissues seems to be very uniform. The absence of ducts, stereids, and sclereids makes the structure quite simple. The epidermis is sparingly hairy or perfectly smooth. The exodermis is thin-walled and consists of one layer of cells pentagonal in cross-section, whose walls are not contractile. The cortex is thin-walled throughout and frequently shows radial collapsing; some of the cells contain druids of calcium-oxalate, but no deposits of starch. The endodermis is thin-walled also and shows the Casparyan spots very plainly; it surrounds a continuous pericambium of a single layer. A few strata of more or less thick-walled conjunctive tissue occur in the center of the stele and between the leptome and hadrome. In the tuberous roots the cork is well represented (*figs. 11* and *12*), and the secondary cortex is compact, though exceedingly thin-walled (*C* in *fig. 10*). The secondary leptome (*L* in *fig. 10*) shows a very few cells, and the hadrome (*H* in *fig. 10*) consists of several wide vessels separated by thin-walled parenchymatic tissue and by very broad rays of radially stretched parenchyma between the mestome bundles.

The section shown in *fig. 10* is from the tuberous root of the young shoot shown in *fig. 2*, upon which a small bud is visible. The root is in its second year and shows the enormous increase in proportion to the very narrow primitive stele with the short rays of hadrome (*PH* and *H*). The other section (*fig. 13*) is from an older and much thicker tuberous root, in which the number of vessels is larger and the leptome much better represented (*L*).

Although parenchymatic tissues attain a high development in these tuberous roots, they were never observed to contain any deposits of starch. It is to be noted also that these tissues are peripheral, surrounding the primitive stele, and that the central portion of the stele has no pith, but only a few strata of conjunctive tissue.

The stem

All the internodes are four-winged, while the body of the stem is cylindric. The cuticle is thin, but wrinkled; the cells of the epidermis are small, and moderately thickened in the wings. Hairs of two kinds are frequent: short and clavate ones (*fig. 9*), and some very long ones, with slender pluricellular stalk and a small globular head, the apical cells being extended into papillae (*fig. 6*); they both represent glandular hairs. The cortex is thin-walled and contains chlorophyll, besides druids of calcium oxalate; no palisades were observed. A thin-walled endodermis surrounds the stele, which is composed of bicollateral mestome strands, with the medullary rays narrow and thick-walled. The inner leptome represents much larger groups than the outer, and an isolated leptomatic strand (*fig. 14*) occupies the center of the pith. This central leptome may be followed through the entire length of the stem, but in the basal internodes it is accompanied by a few vessels which it partly surrounds; thus the structure becomes approximately hadrocentric. The pith is thin-walled and contains neither starch nor druids.

As a member of the Dermomyelodesmeae, Rhexia possesses also some mestome strands in the cortex, and these occur in this species only in the wings, three in each wing and very small, but containing a few elements of leptome and hadrome.

With the exception of an occasional thickening of the cortex in the wings, like a very feeble collenchyma, there is no mechanical tissue; in the basal internodes the epidermis and cortex are thrown off, while the endodermis remains intact and about four layers of pericyclic cork are developed. It is in these internodes that a central mestome strand occurs, with both leptome and hadrome.

The shoot is terminated by a flower whose peduncle, although a direct continuation of the stem, shows a somewhat modified structure. It is cylindric, but wingless, and the cortex contains no chlorophyll. The mestome strands are bicollateral, but the inner leptome forms an almost continuous band close to the hadrome, while in the stem internodes the inner leptome occurs as several distinctly separate strands. No central leptomatic strand was observed in the pith.

The leaf

The structure is bifacial. The cuticle is wrinkled on the upper face, but does not show any prominent striation. Viewed *en face* the lateral cell walls of the epidermis are undulate on the dorsal surface but straight on the ventral; the outer cell wall is moderately thickened, and the lumen of the cells is much wider on the upper than on the lower face. Hairs like those described above are frequent, but the clavate ones occur only on the dorsal face, where the stomata also occur. These are level with the epidermis and are surrounded mostly by four cells of the same structure as the other epidermal cells, that is, the lateral walls are prominently undulate. There is a typical palisade tissue of one layer, and beneath this a pneumatic tissue of about four strata with very wide intercellular spaces. Viewed *en face* the cells of the pneumatic tissue are star-shaped, interspersed with roundish cells containing druids of calcium-oxalate. A very different structure is to be observed in the median portion of the blade, where the very broad midrib is located. The cuticle is here wrinkled on both faces, and the lumen of the epidermal cells is narrow. A large colorless parenchyma forms a broad keel underneath the midrib, and is thin-walled except where it borders the epidermis. No true collenchyma, however, is developed in any part of the blade, and no stereome. The midrib has no parenchyma sheath and contains one broad, arch-shaped, bicollateral mestome strand and a small supernumerary (*fig. 15*). This small mestome strand shows the leptome above the hadrome, and is separated from the midrib by a few strands of colorless tissue.

The very prominent lateral ribs show the same structure as the median, being bicollateral and covered by a colorless tissue on both dorsal and ventral face.

Rhexia mariana L.

All the specimens examined proved to be root-shoots. Some of them were quite young and vegetative, but I was unable to detect seedlings.[6] This species differs markedly from *R. virginica* in possessing no tuberous roots. The roots that produce the shoots are horizontal, very long and slender, and several shoots, both vegetative and floral, may be observed upon the same root; the lateral branches are thinner, lighter brown in color, and branch freely. The shoots in this species are able to persist more than one season, since the buds borne on the basal nodes remain active and produce new shoots in the next year. But, as stated above, young as well as old shoots may be observed among each other on the same root, and consequently on its upper face. Two to four slender secondary roots develop from the basal internodes of the older shoots. No specimen was found in which there was any indication of the primary root, and it would be very interesting to know whether the seedling of this species behaves in the same way as that of *R. virginica*.

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[6] The seedling is described and figured by LUBBOCK in his work on seedlings (1:545), but no mention is made of the further growth or as to the occurrence of root-shoots.

THE INTERNAL STRUCTURE OF THE VEGETATIVE ORGANS

The roots

It is only in the very thin lateral roots that the primitive structure may be observed. The epidermis shows but little tendency to produce hairs; the exodermis consists of a single layer of thin-walled, pentagonal cells that are larger than those of the adjoining cortex. The cortex is of five layers of thin-walled cells, with wide, rhombic, intercellular spaces; druids but no deposits of starch were observed. A thin-walled endodermis and a continuous pericambium surround five groups of leptome, alternating with five short rays of hadrome; while the center of the stele is occupied by a narrow cylinder of moderately thickened conjunctive tissue.

In the thicker and stronger roots, lateral or secondary, the cortex frequently collapses radially, and there is increase in thickness; however they do not increase as much as do the roots of the foregoing species, and never become tuberous. Cork is developed when the secondary leptome and hadrome begin to appear, arising from the pericambium.

As stated above, the roots of this species are very long and grow horizontally and in several cases an excentric growth was noted. In old roots the epidermis and exodermis are partly thrown off, and the cortex is collapsed almost throughout. The stele, however, is protected by four or more strata of cork, within which there are stereids scattered in small groups outside the leptome; the secondary rays of hadrome are relatively short and separated from each other by mostly three rows of thick-walled parenchyma, which also occurs in the central part of the stele. No starch was observed.

The stem

The basal internodes are cylindric; those above are obtusely quadrangular, with four very narrow wings; hairs like those described under the foregoing species cover the stem. The cuticle is very prominently wrinkled, and the epidermis is thin-walled. The cortex is broken down in wide lacunes in the basal internode, but solid in the upper internodes. No collenchyma or stereome was found in the stem. There is only one small collateral mestome strand in each of the four wings, and sometimes one or two between them. The stele represents two arches within the slightly convex faces of the stem, and consists of bicollateral mestome strands with much leptome on the inner face of the hadrome. The pith is thin-walled and does not contain any isolated central strand of leptome; neither druids nor starch were observed. Pericyclic cork is developed, but only in the basal internodes.

The leaf

The cuticular striations over the ventral epidermis (*figs. 8* and*16*), which radiate toward the center of the outer cell wall, are characteristic of the leaf structure. The lumen of the epidermis is considerably wider on the ventral surface than on the dorsal, and the stomata (*fig. 7*) are not confined to the latter. They show the same structure as those of the other species, and some were noticed on the ventral face of the leaf-blade. Hairs of both kinds described above are scattered over both faces, and also along the margins. The chlorenchyma shows the same structure as observed in *R. virginica*, but the pneumatic tissue is less open. The midrib lacks the supernumerary ventral mestome strand, but otherwise the structure of the veins is identical with that of the former species.

Summary

Considered from an anatomical point of view, these two species may be distinguished from each other by the following contrasting characters:

R. virginica.—Roots tuberous where the shoots develop; no stereids outside the leptome of the root; stem broadly four-winged, with three mestome strands in each wing; one central mestome strand in the pith; no cuticular striations above ventral epidermis of leaf;

stomata only on dorsal face; midrib with a supernumerary mestome strand; clavate glandular hairs on dorsal face of leaf.

R. mariana.—Roots slender throughout; stereids outside the leptome of the root; stem narrowly four-winged, with one mestome strand in each wing; no central mestome strand in the pith; cuticular striations very distinct above ventral epidermis of leaf; stomata on both faces of leaf; midrib without a supernumerary mestome strand; clavate glandular hairs on both faces of leaf.

Common to both species are the bicollateral mestome bundles of stem and leaf; the absence of specialized subsidiary cells around the stomata; the absence of mechanical tissues (stereome and collenchyma); the occurrence of two types of glandular hairs; the bifacial structure of the leaves; and the ability of the roots to produce shoots.

Vegetative propagation, therefore, depends upon the development of root-shoots, and, upon examining herbarium material, the same mode of propagation was found in *R. lutea* Walt., in which the roots are very long and slender, and the base of the shoot may persist for more than one season, *R. lanceolata* Walt., *R. serrulata* Nutt., and *R. ciliosa* Michx. All agree with *R. mariana* in the roots being slender and able to produce shoots. In *R. serrulata* one specimen appeared as if it was a seedling and blooming in the first season; and one specimen of *R. floridana* Nash had a tuberous root in addition to the slender, shoot-bearing root.

I believe that Rhexia must be placed with that type of plants in which the production of root-shoots is necessary to the normal development of the individual. It is a type poor in representatives, and WITTROCK enumerates species of Cirsium, Linaria, Convolvulus, Thesium, Coronilla, Epilobium, and Euphorbia as representing it. *Thladiantha dubia* Bge. doubtless belongs to this same category, according to SACHS,[7] who states that "the yearly regeneration is dependent upon root-shoots which develop from tuberous swellings of the very long and slender roots." The internal structure of the roots of this curcurbitaceous plant is described by SCOTT and BREBNER,[8] but is very different from that observed in Rhexia.

BROOKLAND, D. C.

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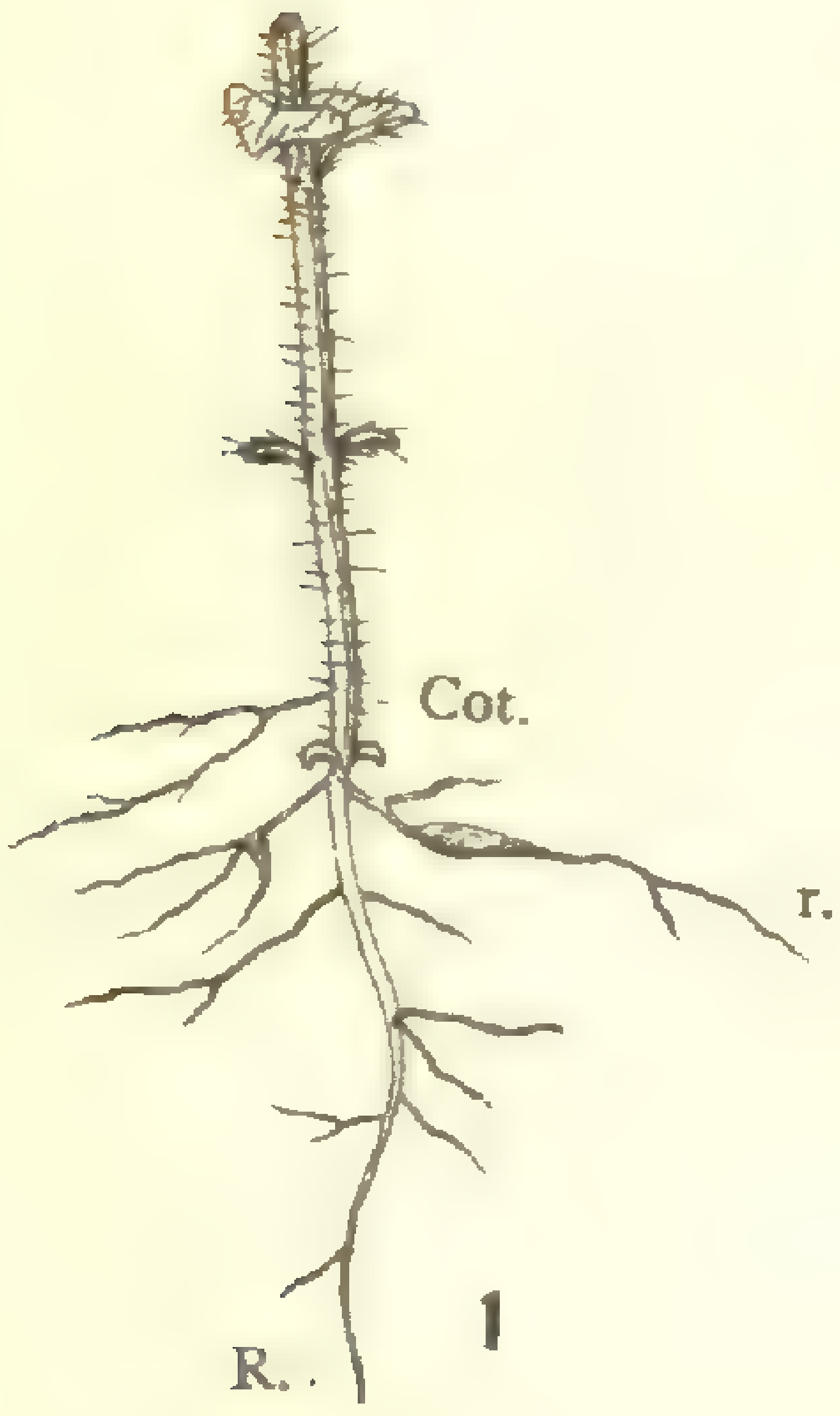
[7] Vorlesungen über Pflanzen-Physiologie 28. Leipzig. 1882.

[8] Annals of Botany 5:273. 1890.



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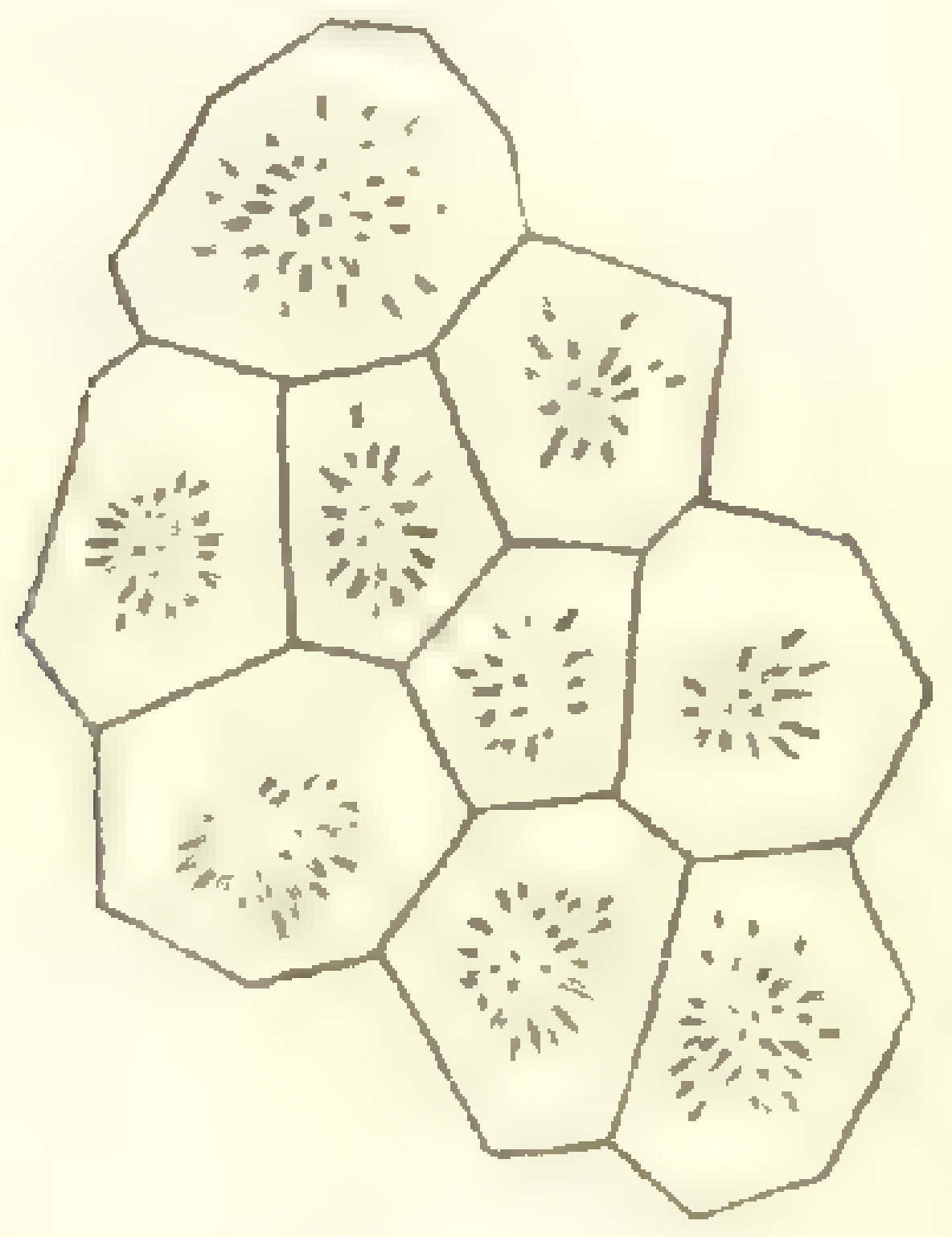

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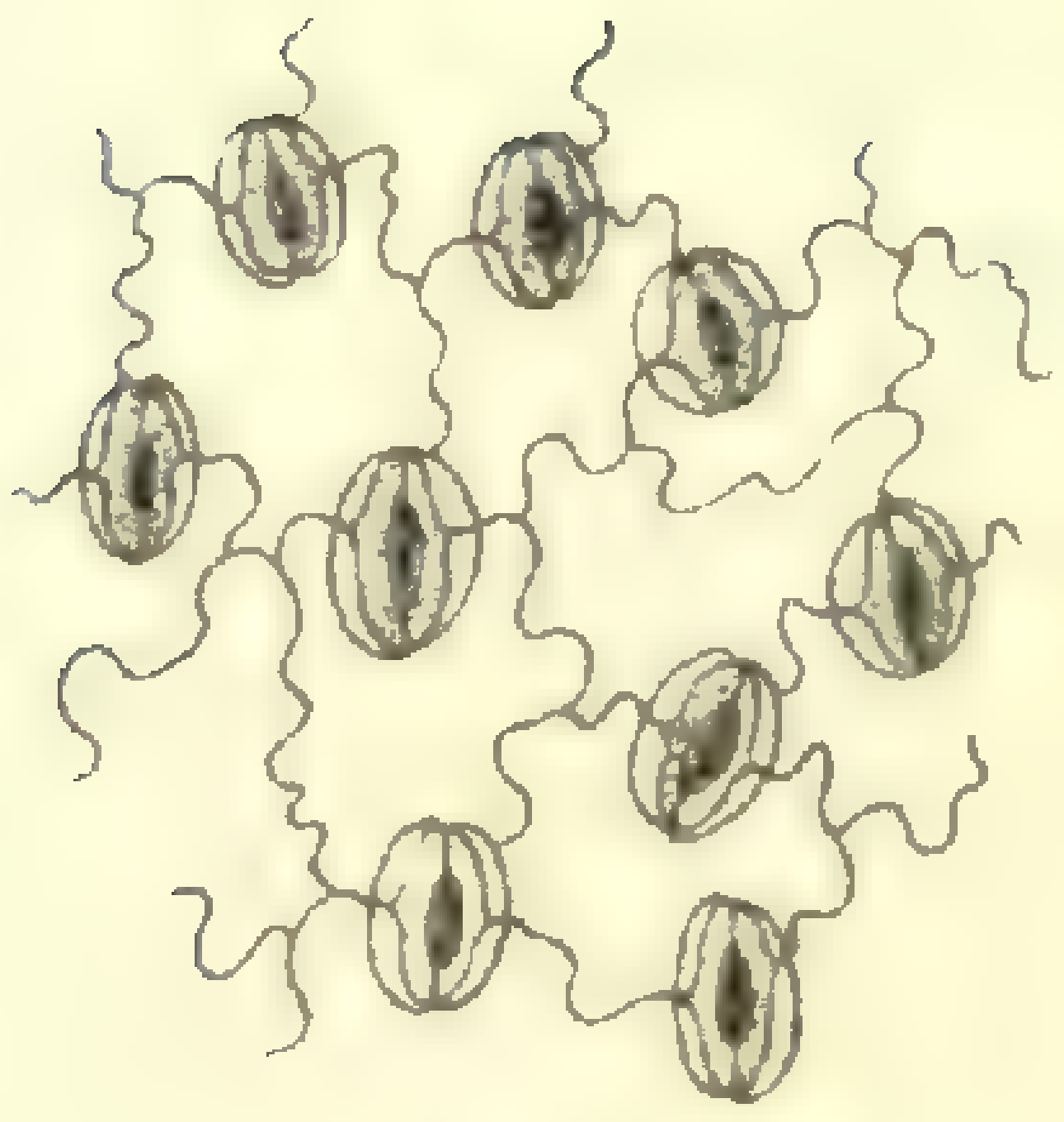

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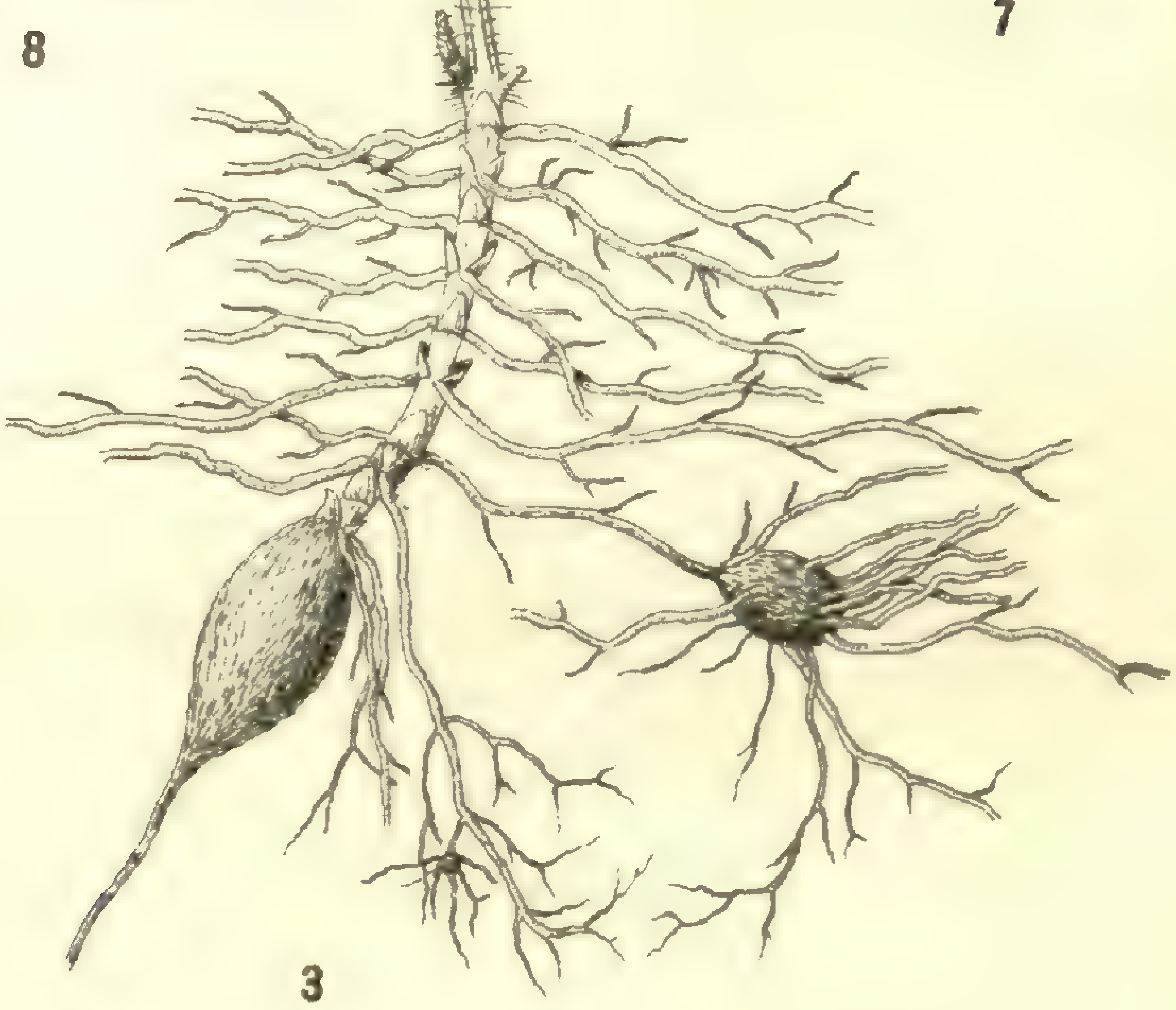

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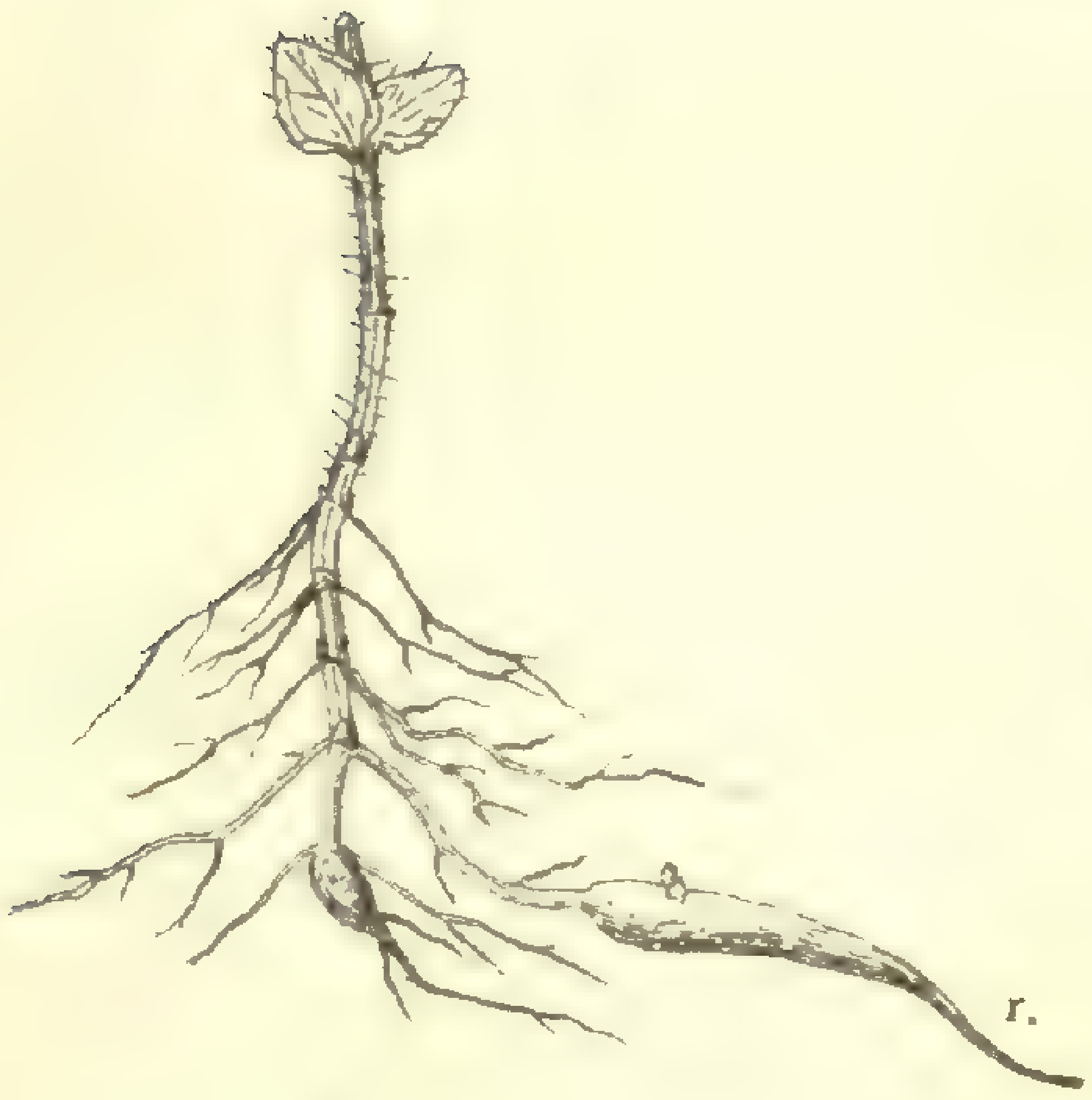

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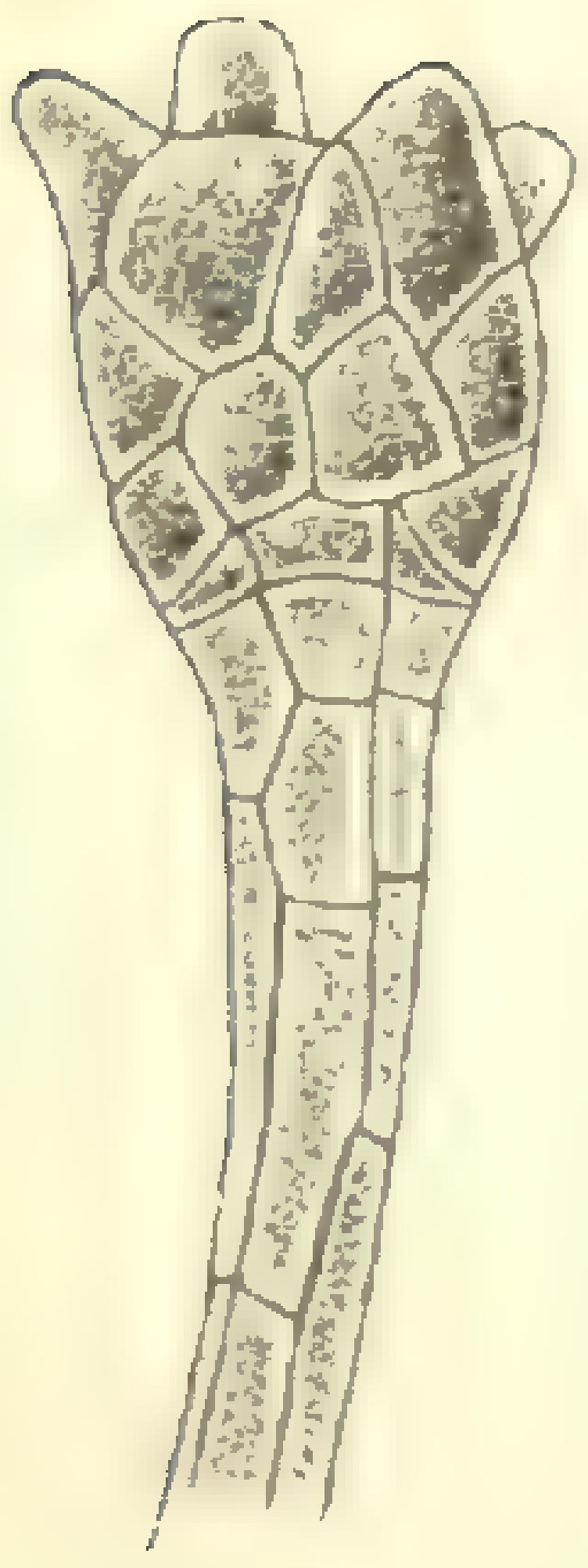

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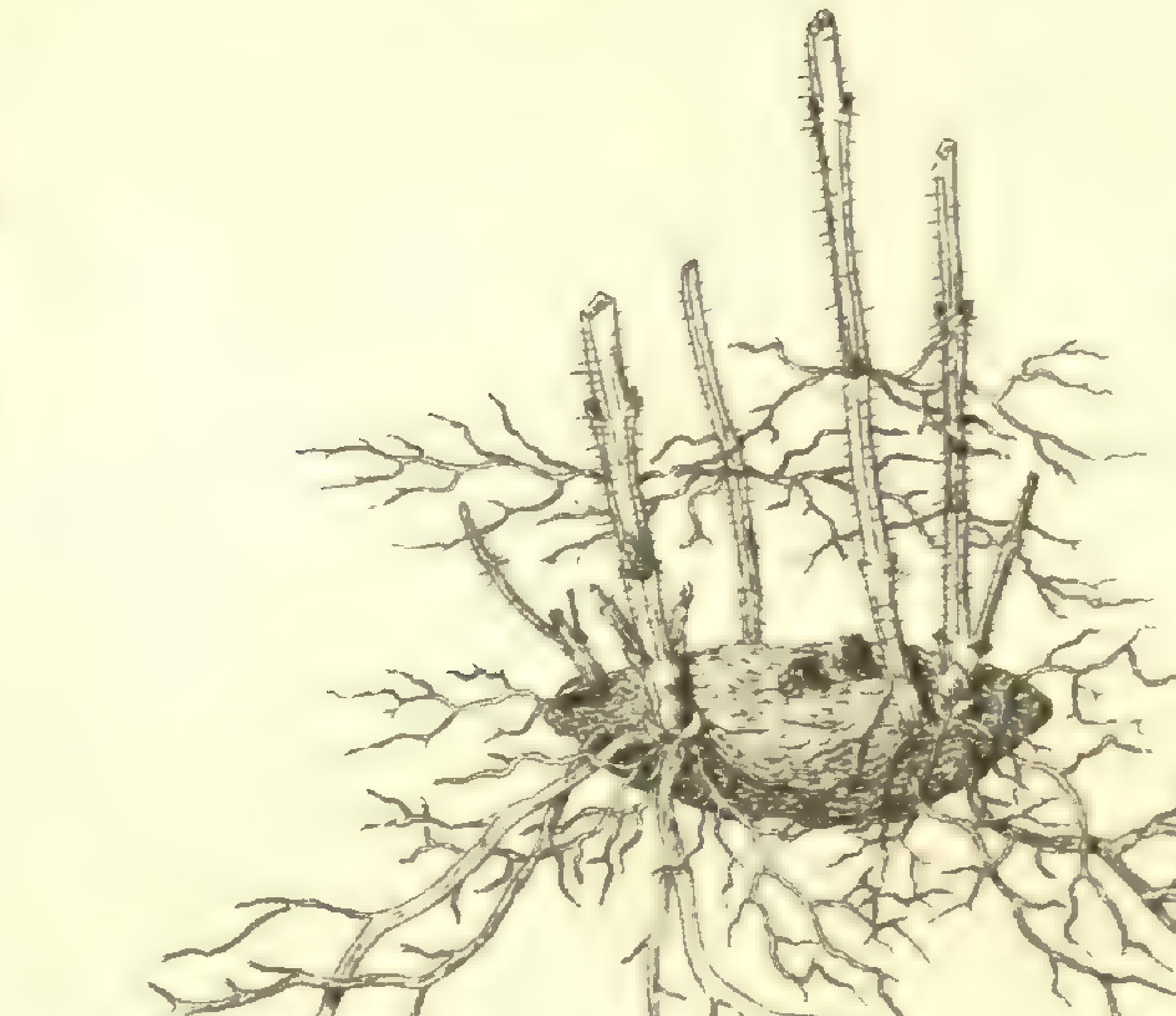

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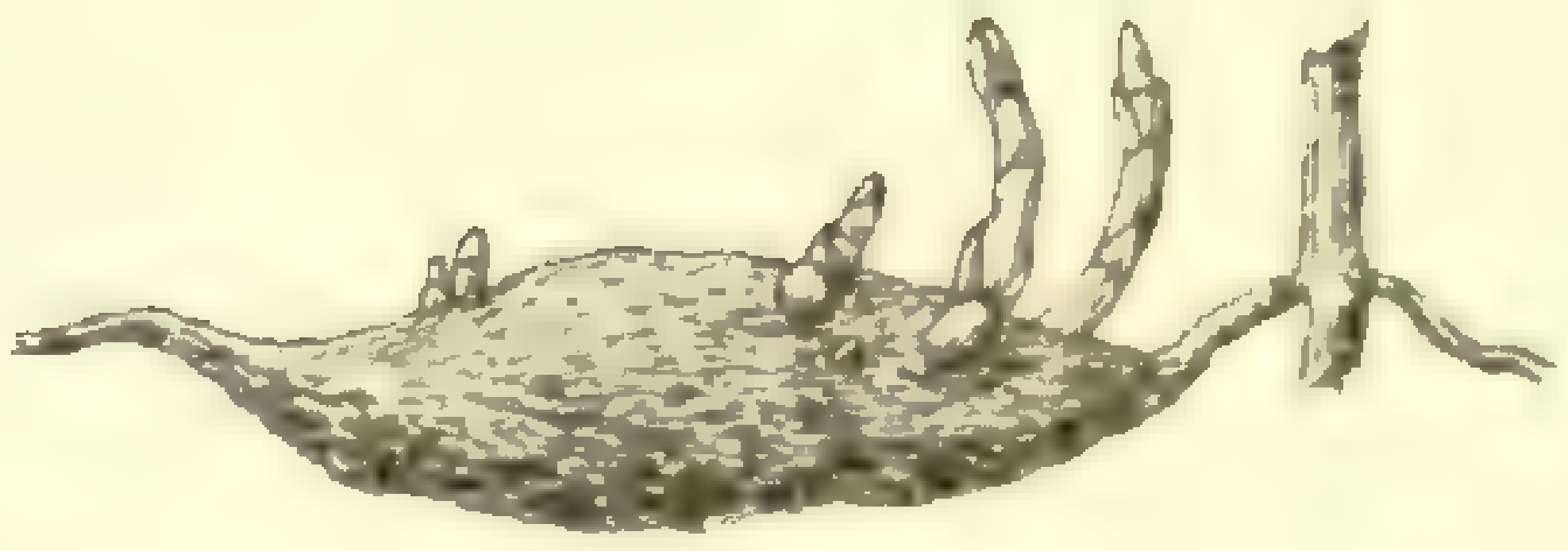

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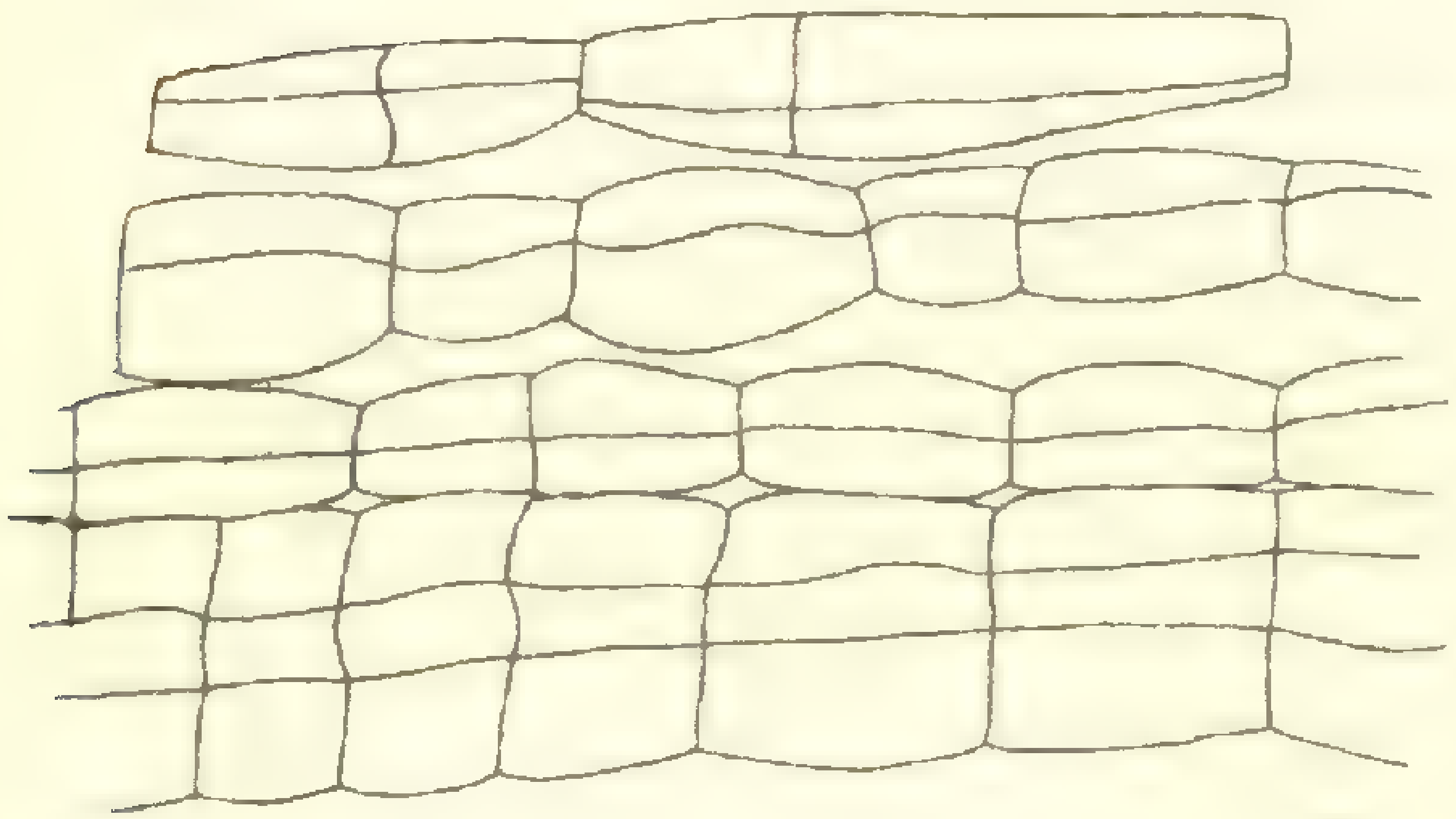
Auctor ad nat. delin.

HOLM on RHEXIA



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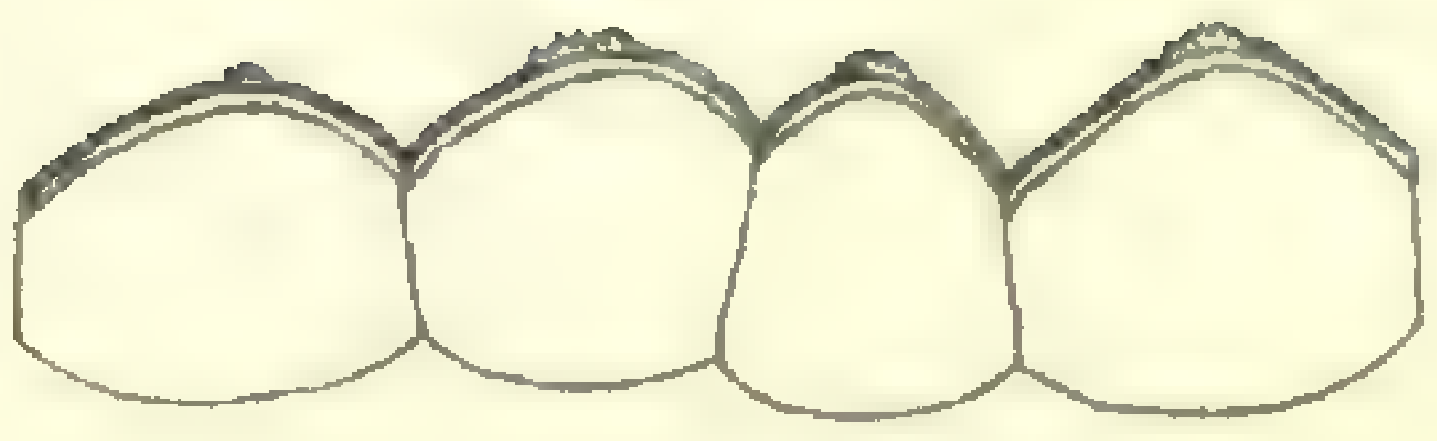

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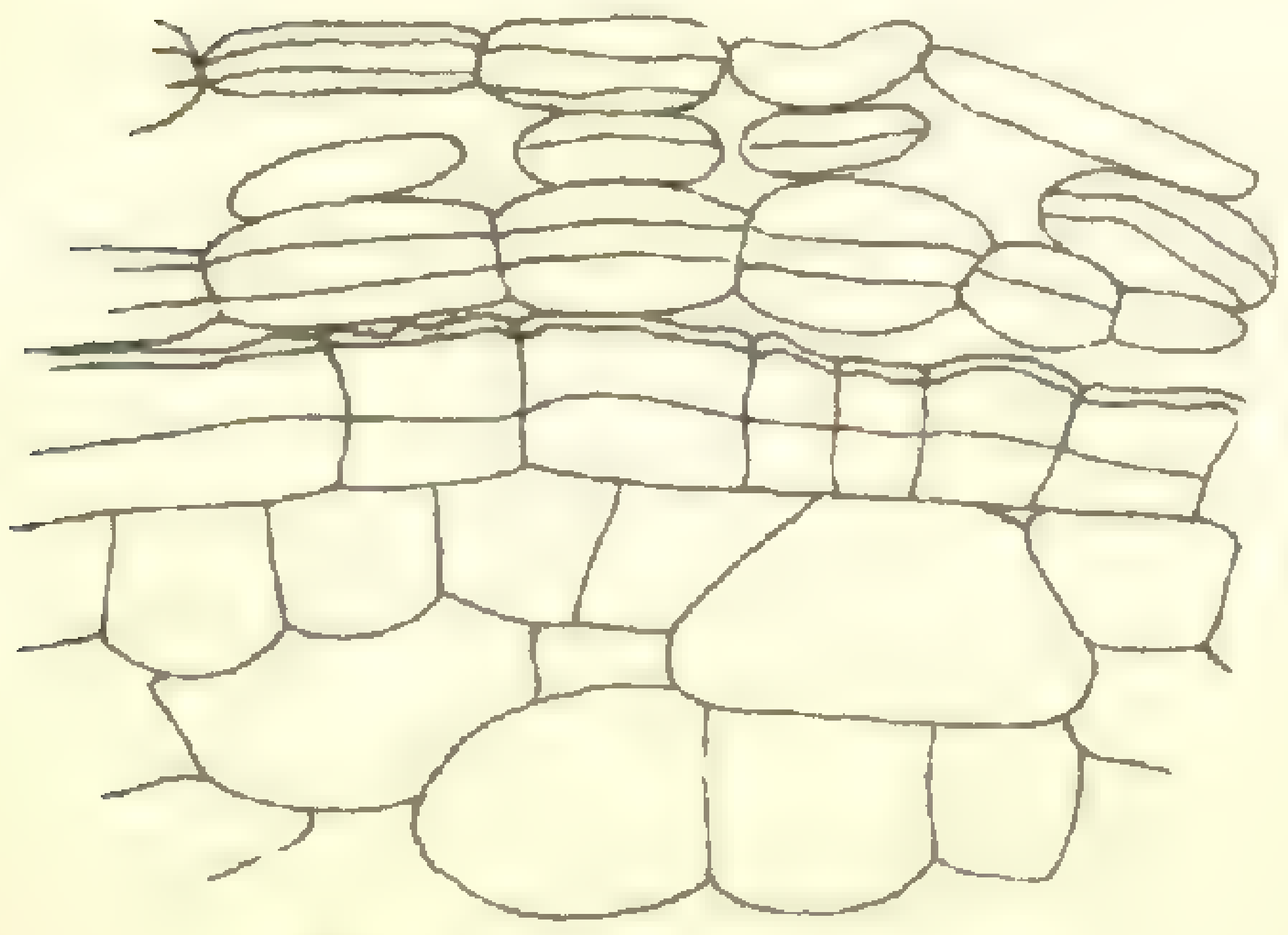

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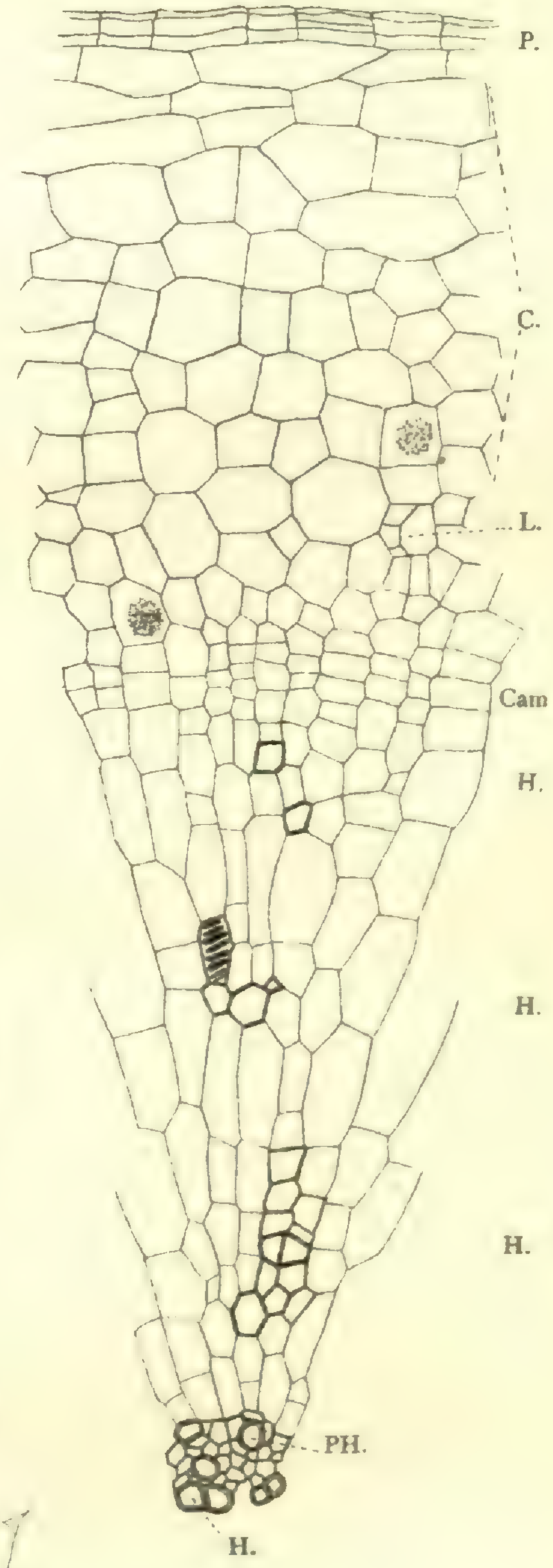
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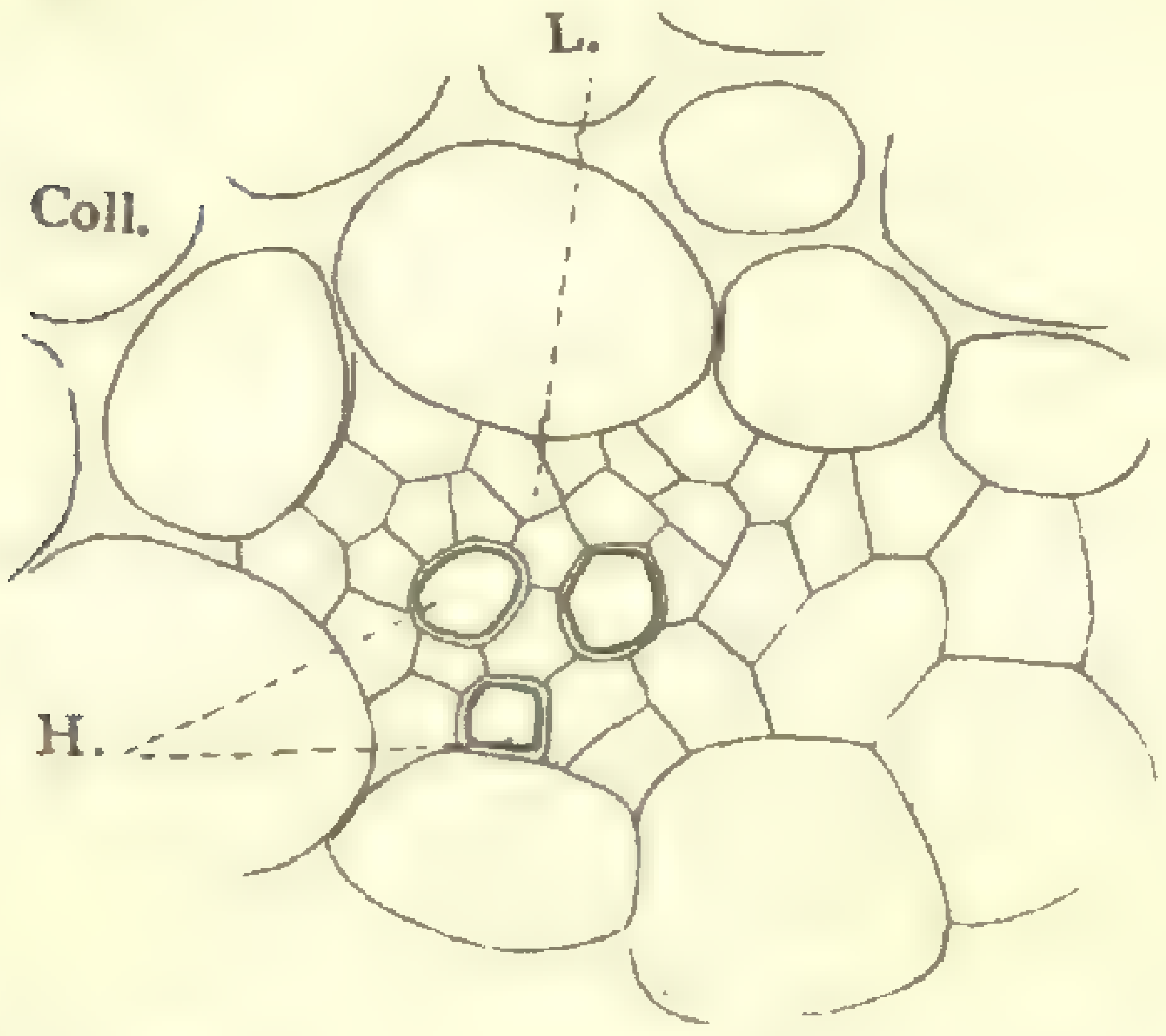

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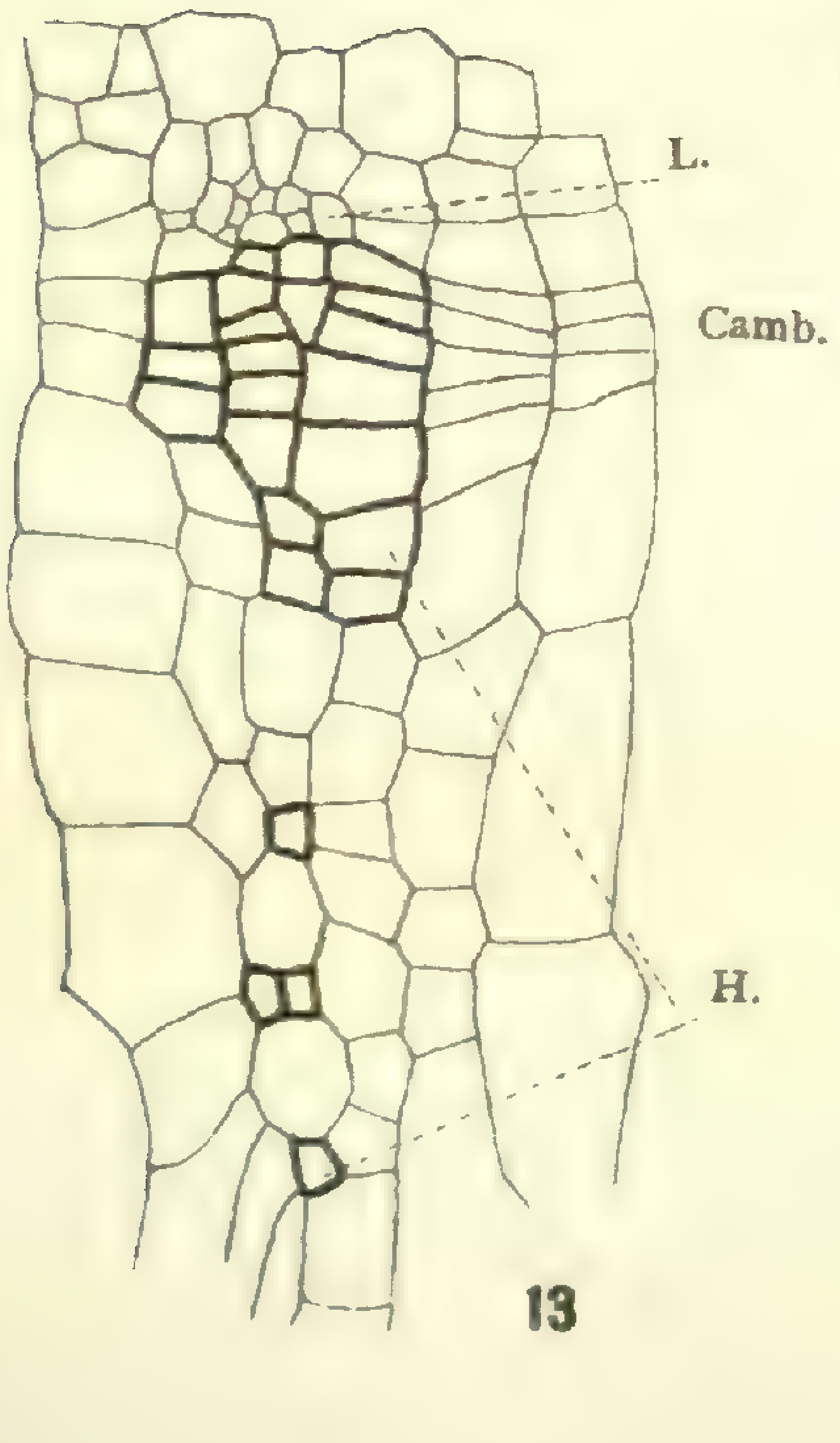

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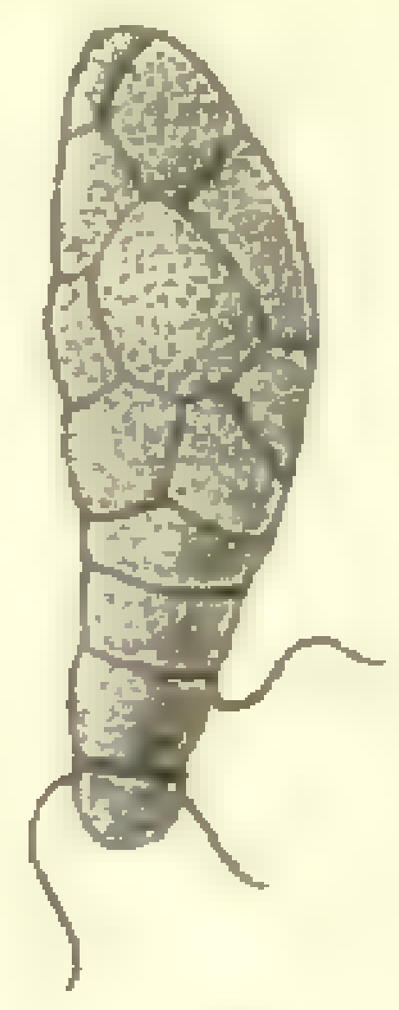

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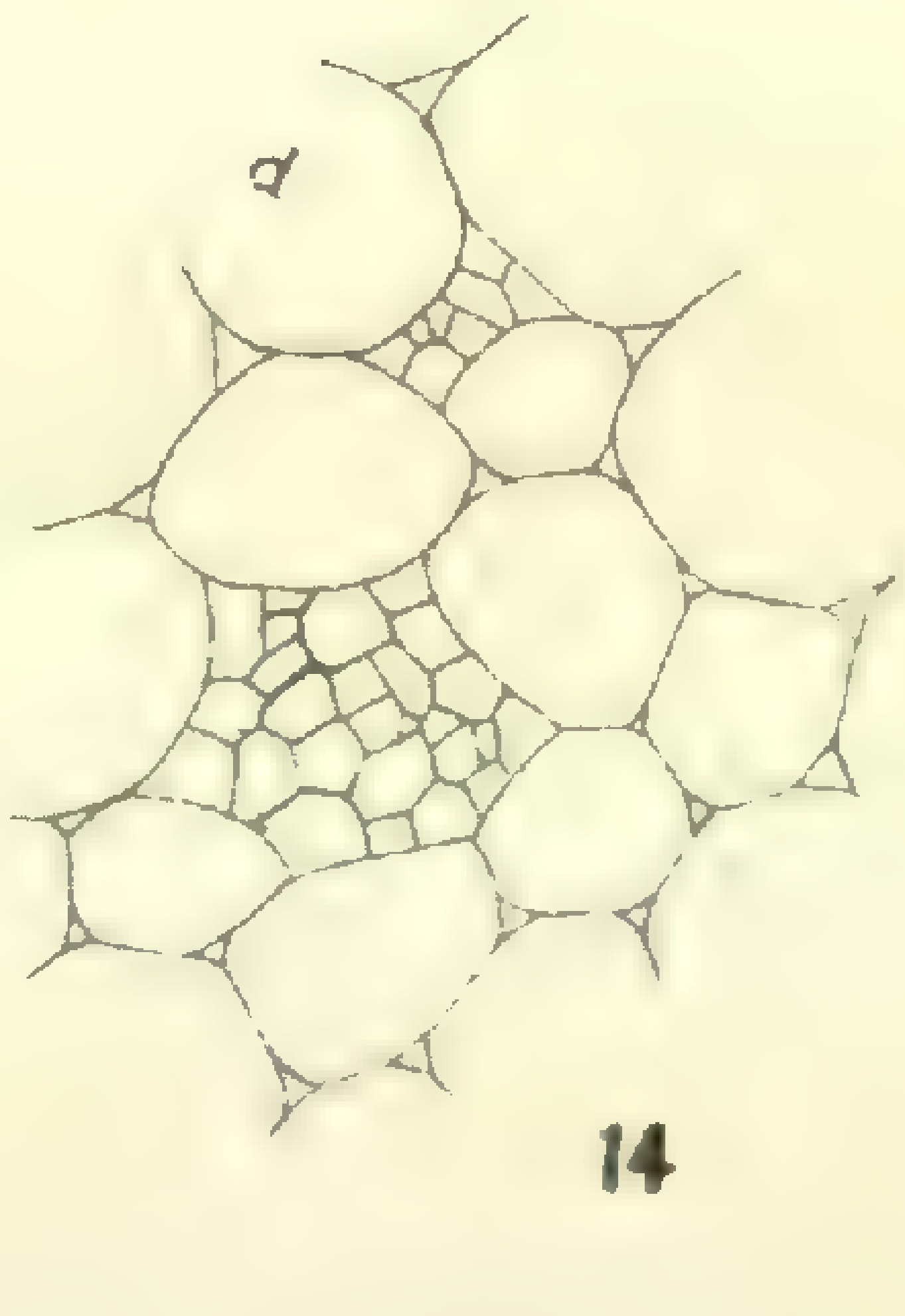

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Auctor ad nat. delin.

HOLM on RHEXIA

EXPLANATION OF PLATES I AND II

PLATE I

Rhexia virginica

FIG. 1. Seedling, showing basal internodes, cotyledons (*Cot*), primary root (*R*), and a lateral root with the tuberous swelling (*r*). ×1⅔.

FIG. 2. A root-shoot developed from tuberous root of seedling; a lateral root swollen (*r*) and showing bud which will develop a shoot during next season. Natural size.

FIG. 3. The underground portions of a mature root-shoot; one of the secondary roots bears a tuber. Natural size.

FIG. 4. An old tuber with shoots. Natural size.

FIG. 5. An old tuber with buds. Natural size.

FIG. 6. Apex of a long glandular hair. ×320.

PLATE II

Rhexia mariana

Fig. 7. Epidermis of lower face of leaf. ×320.

FIG. 8. Epidermis of upper face of leaf. ×320.

Rhexia virginica

FIG. 9. Glandular hair. ×320.

FIG. 10. Transverse section of the tuberous root of *fig. 2*, showing cork (*P*), secondary cortex (*C*) with druids, leptome (*L*), cambium (*Cam*), hadrome (*H*), and protohadrome (*PH*). ×204.

FIG. 11. Cork of the same tuber. ×320.

FIG. 12. Cork of an older tuber. ×320.

FIG. 13. Transverse section of an old tuber, showing outermost part of a mestome strand; index letters as above. ×320.

FIG. 14. Central leptome strand of stem. ×320.

FIG. 15. Ventral supernumerary vein of leaf, also showing thick-walled colorless tissue (*Coll*), leptome (*L*), and hadrome (*H*). ×560.

FIG. 16. Transverse *Rhexia mariana* section of ventral epidermis of leaf. ×320.

THE SPORANGIUM OF THE OPHIOGLOSSALES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCIV

L. L. Burlingame

(WITH PLATES III AND IV)

The sporangium of the Ophioglossales has been studied by Russow (**'92**), Goebel (**'80, '81**), Holtzman (**'92**), Rostowzew (**'92**), Campbell (**'95, :05**), Bower (**'96**), Cardiff (**:05**), Stevens (**:05**), and Beer (**:06**). Of these the last three concern themselves almost wholly with the later stages of the development of the sporangium and with the development of the spores up to the time of shedding. The former investigators devoted their principal attention to the early stages of sporangial development. Of their accounts, Bower's is the most comprehensive and, so far as the earlier stages of Ophioglossum are concerned, the most satisfactory.

In the fall of 1906 there came into my hands, through the courtesy of Professor John M. Coulter and Dr. Charles J. Chamberlain, some fertile spikes of *Ophioglossum reticulatum*, which had been collected by Dr. H. N. Whitford at Lamao, Bataan, Philippine Islands. The spikes, from plants growing at an altitude of seventy-five feet above sea level, were collected July 26, 1904, killed and fixed in chrom-acetic acid, run up through the alcohols to 70 per cent., and sent to Chicago.

With the completion of this investigation each of the three genera of Ophioglossales will have been studied throughout the entire period of development of the sporangium and spores up to the time of shedding, so that a discussion of the development of the sporangium in the group seems timely. In this discussion Ophioglossum will be made the type, with frequent comparison with the other genera. The material of *O. reticulatum* showed no stages earlier than those represented in *figs. 1* and *8*, where the wall is about three-layered, the tapetum one-layered, and the sporogenous tissue about two divisions short of the mother-cell stage. This renders it necessary to obtain the account of earlier stages from the writings of former investigators.

Earlier stages

OPHIOGLOSSUM

According to BOWER, the first indication of the regions from which sporangia are to form is the differentiation along each side of the spike of a band about two cells wide. The cells of this band are distinguished from their neighbors by a greater depth, a difference in arrangement, and differences in cell contents. He calls this the sporangiogenic band. The cells are for the most part arranged in pairs, but he does not regard this as sufficient evidence of their common origin, for he says that if the cells concerned in forming a single sporangium originate from a single cell, it must be very early in the formation of the spike. Nor did he succeed in distinguishing them at a stage so early as to enable him to trace their origin. At a slightly earlier stage, GOEBEL figures the band as only in part two cells wide. His figure seems to support his contention that the band becomes two cells wide by the longitudinal anticlinal splitting of the cells of a band but one cell wide. Some of BOWER'S figures show a far less regular arrangement of the cells in the band. In these cases, as he clearly points out, it is much less easy to refer the origin of the band to a single row of cells. It is not unlikely that the difference of opinion is due to the recognition of the band at slightly different stages in the growth of the sporangial spike, for it is not unusual for subsequent growth to displace cells so as to render their relationship to one another obscure. Whatever may be the exact mode of origin of this band, the really important point is that sporangia may arise in any part of it, though in fact they do not arise in all parts of it. It is this partial sterilization of a band potentially sporangiogenic throughout on which BOWER lays special stress.

The cells of this sporangiogenic band divide periclinally, separating a potentially primary sporogenous band from the wall cells. According to BOWER, each archesporium consists usually of a single pair of the cells of the band; where the band is three cells wide, there are three cells in the archesporium. GOEBEL, with whom CAMPBELL agrees, thinks the archesporium is unicellular. ROSTOWZEW also claims a unicellular archesporium, but RUSSOW contends that it is a cell-complex. From such divergent opinions the truth is difficult to choose, though it seems not unlikely that the band may be recognizable while only one cell wide, and that the first division in each cell is periclinal and cuts off the potentially sporogenous cells from the ones destined to form wall and tapetum. The outer segments, according to BOWER, by repeated division add considerably to the sporogenous tissue. It is specifically stated by BOWER and ROSTOWZEW, and implied by CAMPBELL, that the tapetum arises from the outer part of the sporogenous tissue.

The species studied were *O. pendulum*, *O. vulgatum*, *O. reticulatum*, by BOWER; *O. pendulum* by CAMPBELL; and *O. vulgatum* by GOEBEL and ROSTOWZEW.

HELMINTHOSTACHYS AND BOTRYCHIUM

In *Botrychium virginianum* HOLTZMAN figures the sporangium as arising from a single cell. Writing of Helminthostachys, BOWER says: "The sporangia are similar in origin and mature structure to those of Botrychium, the essential parts being referable to a single superficial cell, of which the first periclinal division defines the sporogenous from the protective parts." In agreement with RUSSOW he thinks that in at least some species of Botrychium the archesporium may consist of more than one cell. GOEBEL and CARDIFF think the archesporium in *B. lunaria* and in *B. virginianum* is one-celled. CAMPBELL likewise thinks that the archesporium of Botrychium is a single cell and that the entire sporangium is referable in origin to this one superficial cell. He ascribes the origin of the tapetum partly to the wall and partly to the outer sporogenous tissue. GOEBEL figures it arising from the wall and sterile cells surrounding the sporogenous tissue. CARDIFF also is positive that it comes wholly from the wall and tissue outside of the sporogenous mass. In Helminthostachys BOWER has shown that the sporangium originates from a single superficial cell, that there is a single primary sporogenous cell, and that the tapetum arises from the wall.

Later stages

The preceding account brings the development to the earliest stages shown in the writer's material, the discussion of which may be taken up conveniently under three heads: the wall, the tapetum, the sporogenous tissue.

THE WALL

Owing to the conflict of opinions, the youngest material at hand was examined for evidence of the origin of tapetum and sporogenous tissue. These sporangia have a wall three cells thick, or in some cases the spindle and beginning of the wall between the middle and innermost cell. *Fig. 1* shows the next stage, where the wall is three or four cells thick. Where the wall is four cells thick and the position of the walls indicates the last one formed (wall *1* in the figure), the division is seen to have occurred in the outer cell of the three-layered wall. The fifth layer of cells also arises in a similar way by the division of the cells of the outer layer of a four-layered wall (*figs. 2* and *3*, wall *1*). This is made clearer by an examination of the cell row between the two containing five each in *fig. 2*. It may be seen that the next division will occur in the outer cell.

The order of development may be stated in the reverse order as follows: If the cell layers be numbered from within outward *1, 2, 3, 4, 5*, then *5* and *4* arose from the division of a cell which we may call *c*. In like manner *c* and *3* arose from the division of a cell *b*. As already pointed out, *1* and *2* arose from the division of a cell *a*. The tapetum is already formed and differentiated at the two-layered stage of the wall, so that two suppositions may be entertained in regard to the early history of the wall. First, *a* and *b* may have been derived from the division of a cell *w*, sister to the tapetal cell. Second, cell *a* and the tapetal cell may be sister cells derived from the division of a cell sister to *b*. Of these two suppositions, both of which assume the tapetum to have originated from the wall, the former seems the more probable. That the tapetum does arise from the wall seems to be indicated by the close similarity of its cells in shape and position to the tabular wall cells and their contrast to the polygonal sporogenous cells. In the very earliest stages observed it is difficult to distinguish tapetal cells from wall cells except by position, though the sporogenous cells are easily distinguishable in almost all cases. It is not unlikely that the first division of the cell (or perhaps cells) of the sporangiogenic band is a periclinal one and separates the primary sporogenous from the primary wall cell. A periclinal division of the latter separates the primary tapetal cell from the wall cell, subsequent divisions of which produce the five-layered wall. If this interpretation be accepted, then Ophioglossum agrees with the other genera in the origin of sporangium, wall, primary sporogenous cell, and tapetum.

This regularity of division is limited to the part of the outer wall which from its position may be inferred to have arisen from the sporangiogenic band. In other parts of the wall, not only is the division less regular, but the number of layers is greater. Furthermore, longitudinal sections show that probably this regularity is still further limited to the cells derived from the initial cell (or cells) of the sporangium.

By the time the sporogenous tissue has reached the mother-cell stage, the wall has its full number of cell layers. The further development of the wall consists of an increase in size of the hypodermal cells in the tangential plane, without any increase of thickness, and a growth and anticlinal division of the epidermal cells. In mature sporangia the epidermal cells are relatively deep and narrow, with thickened outer walls. *Fig. 7*, which shows a sporangium at time of dehiscence, may be compared with *fig. 6*, from a sporangium whose sporogenous tissue had reached the stage of young tetrads. *Fig. 7* has just half the magnification of *fig. 6*, from which it is evident that the epidermal cells have just about doubled their depth, and have in some cases decreased in width through anticlinal division. As already remarked, the hypodermal cells do not increase in thickness, but become extended laterally as the sporangium enlarges. From about the time the young spores begin to round up, they gradually lose their cell contents and become flattened as growth of the sporangium progresses. Sooner or later the walls of the inner two or three layers, and often all the hypodermal layers, disappear. In *fig. 7* portions of the walls of two layers can be traced, but in other cases the only remains consist of a line of débris between the spore-mass and the epidermis.

At the earliest stage examined, the wall cells contain considerable starch, which increases up to the time the wall has attained its full number of cell layers. After this, which is about the time the tapetal plasmodium invades the crevices of the sporogenous tissue, it gradually wastes away, until none at all is present at time of dehiscence. Its disappearance may be connected with the accumulation of starch in the tapetal plasmodium, a matter which will be discussed subsequently.

Longitudinal sections (*figs. 6* and *7*) show the method of dehiscence. About the time the young tetrads are forming, each sporangium shows a slight transverse groove. *Fig. 6* shows that this corresponds to a band of smaller thin-walled cells. The groove becomes more pronounced through the failure of the epidermal cells along it to increase in depth as fast as the neighboring ones. Finally a rupture of the sporangium occurs along this groove, probably due to strain set up by unequal growth. The spores are shed through this slit, which, so far as the material at hand indicates, seems to play a purely passive rôle in the process.

THE TAPETUM

The youngest stage of the tapetum observed is shown in *fig. 1*. That this probably originates from the first periclinal division of the primary wall cell has already been pointed out. It divides periclinally once (sometimes oftener, as shown in *fig. 5*), before the cells of the sporogenous tissue have reached the mother-cell stage. Usually no more strictly periclinal divisions occur. As the sporangium grows, the tapetal cells elongate and divide obliquely (*figs. 2, 3, 5*). *Fig. 3* presents a regional view of about one-half of a sporangium with the tapetum well developed and distinct at the left of the figure, where it may be supposed to be derived from the primary wall cell. At the right of the figure the tapetal cells are not easily distinguished from the sporogenous tissue, and their origin is not clearly indicated, though they seem rather more closely related structurally to the sporogenous cells than to the sterile cells around them on the outside. In Botrychium GOEBEL has shown that this part of the tapetum arises from the sterile cells outside the archesporium. In the present study no clear evidence for either view was obtained, owing to lack of young sporangia.

At the earliest observed stage the tapetal cells are distinguishable from the sporogenous tissue by staining reactions of the cell contents and by the position of the walls. They are less easily distinguished from the wall cells, but are on the whole slightly thicker radially. The cytoplasm is clear and highly vacuolate and so takes the stain lightly. It does not contain starch nor any form of stored food evident under the microscope. In this respect it differs from the cytoplasm of the inner wall cells, which even at this stage contain a little starch; the outer wall cells contain considerable at this time. The tapetal cytoplasm was not observed to contain any starch until after the walls have broken down. The walls themselves are from the first very delicate, but are sharp and distinct when properly stained, so that there can be no mistake as to their presence. In this respect Ophioglossum seems to differ from *B. virginianum*, whose tapetal cells, as described by STEVENS, are delimited by a plasmatic membrane only. CARDIFF, who studied the same species, does not mention this circumstance, and BEER calls attention to the fact that it is not true in Helminthostachys. The nuclei are about 20 μ in diameter, but vary somewhat both in size and shape. They stain rather deeply and are generally not otherwise distinguishable from the nuclei of the wall cells.

When the mother-cell stage is reached, the tapetum is at least two-layered throughout and its walls have become very thin and about this time have begun to break down. The cytoplasm of the neighboring tapetal cells mingles and forms a plasmodium, as described by CARDIFF for Botrychium. In Botrychium as well as in Helminthostachys the tapetal cells are elongated radially, while in Ophioglossum they are flat and tabular, the radial diameter being the shortest. Ophioglossum also differs from the other genera in having usually only two layers of tapetal cells, whereas they have from two to four layers. It seems likely that the walls break down sooner in Ophioglossum than in the other genera. This is probably correlated with the fewer layers and with the fact that in Botrychium the cells are frequently binucleate. Too few preparations at just the stage when the walls are breaking down were seen to make sure that binucleate cells do not occur, but none were seen.

BOWER and others have stated that at this time some of the mother cells break down and contribute to the tapetal plasmodium. This is denied by CARDIFF for Botrychium, and by BEER for Helminthostachys. No certain case of such a contribution was observed in Ophioglossum, but the number of preparations of just this age observed were too few to justify the statement that it never occurs. Mother cells which did not appear normal were found in two or three preparations, but in each case they occurred in sporangia that were in other respects clearly abnormal, suffering from external injury to the wall in one case, an abortion of the inner wall cells and neighboring sporogenous tissue in another, etc. In sporangia apparently normal in all respects, a few of which were observed, no trace of such a contribution was found. It is not unlikely, therefore, that this genus agrees with the other two in this feature also.

At the time the plasmodium begins to penetrate among the crevices of the sporogenous tissue they are rather small, and the movement is therefore gradual. Hence the deeper parts of the crevices are empty of cytoplasm. By the time the sporangium has reached the stage shown in *fig. 4*, the plasmodium completely fills every crevice, showing that the cytoplasm increases in volume after the breaking-down of the walls. The nuclei do not at first penetrate among the blocks of sporogenous tissue on account of the narrowness of the clefts, but later as these enlarge they become distributed throughout the sporangium.

The structure of the plasmodial cytoplasm is at first coarser and stains more deeply than did that of the tapetal cells before the breaking-down of the walls. It has a ropy appearance and contains many large granules. It does not seem to be definitely vacuolate, but among the beaded threads there seems to be a fine hyaline sap-like substance (*fig. 4*). At this time the plasmodium does not contain any starch, which, however, soon appears and continues to increase until the plasmodium is fairly crowded with it (*fig. 16*). The stringy cytoplasm becomes denser during the formation of the starch and finely vacuolate. The maximum density and starch content is reached about the time the tetrads are complete. From this time on the starch grains become fewer and fewer (*fig. 25*) until they have entirely disappeared. By this time the cytoplasm, which has been growing more and more vacuolate, has nearly all disappeared. The last traces of it are to be seen along the old plasmatic membranes, which may often be traced long after the more fluid parts have disappeared. When the spores are of the age shown in *figs. 26* and *27* all traces of it are usually lost.

The nuclei of the plasmodium exhibit frequent changes of form in order to accommodate themselves to the spaces which they are compelled to occupy, or into which they perhaps force themselves. Where one is found in a narrow cleft it has the appearance of being about to divide amitotically. No actual case of such amitosis, however, has been observed in any stage of the tapetum. No mitotic figures have been observed in the plasmodium either, though the nuclei seem somewhat more abundant in the later stages. The sporangia vary so much in size and consequently in number of nuclei found at any stage that it is not possible to say with confidence that the nuclei increase after the walls of the tapetum have disappeared. That the nuclei do not move about passively in currents of cytoplasm seems to be indicated by the fact that where one is apparently just entering a crevice it is always drawn out to a point, which stains more deeply with chromatin stains than do the other parts of the nucleus. BEER has called attention to similar appearances of the nuclei of Helminthostachys. The average size of the nuclei does not differ materially in older stages from that of the earlier ones. There is considerable individual variation of both size and shape at any stage. CARDIFF has pointed out that the nuclei of the plasmodium of Botrychium increase fourfold in size; but BEER has found that this is not the case in Helminthostachys. The structure of the nucleus, however, does undergo considerable change. A reference to *fig. 16* shows the tendency of the chromatic material in the later phases of development to aggregate itself into elongated masses, whose long axes are directed lengthwise of the nuclei. These masses are much fewer than the chromosomes. A similar condition is shown in BEER'S figures of Helminthostachys. When the nuclear membrane breaks down, these masses are spilled out and persist for some time. The nuclei persist longer than the cytoplasm; it is not uncommon to find one or more of them in sporangia from which the spores are just about ready to be shed.

THE SPOROGENOUS TISSUE

The earliest stage of the sporogenous tissue observed is shown in *fig. 8*. At this time it probably lacks about two divisions of the mother-cell stage. The cells are squarish or polygonal, and about 25 μ in diameter. The nuclei, which vary slightly, average about 18 μ in diameter. The cytoplasm is delicately reticulated and does not stain very intensely. It seems to be made up of a network of delicately beaded strands, the meshes of which are filled with a hyaline ground-substance which stains very lightly or not at all. The wall is very thin but distinct. **Stevens** reports the sporogenous cells of Botrychium as being devoid of a wall. The cells at this stage, in the living condition, are probably still attached to one another so as to form a compact tissue. In stained preparations clefts appear among groups of cells. It is probable that some or all of these clefts are the effects of contraction in the preparation of the material. The nucleus is usually quite round and is surrounded by a sharply defined nuclear membrane. The nuclear network is not very unlike that of the cytoplasm, except that the beaded strands are larger, stain more deeply, and present many more loose ends. From one to six nucleoli are usually present in each nucleus.

Whether the blocking of the sporogenous tissue begins as early as the stage shown in *fig. 8* or not, there is no doubt that it is clearly present after the next division of the sporogenous cells. Such a condition is shown in *fig. 2*, where the sporogenous tissue is seen to be broken up into irregular blocks, and to be free from the tapetal cells, which are beginning to separate from one another. *Fig. 3* presents a view of a slightly more advanced state of blocking. The irregularity of Ophioglossum is in sharp contrast to the almost diagrammatically regular blocking of the sporogenous tissue of Botrychium. According to **Cardiff**, the division of the sporogenous tissue in that genus is in three planes at right angles, and very regular and uniform in all parts of the sporangium. He suggests that these walls break down in the order of their formation, with the result that the tissue breaks up into regular rectangular blocks. His figures lend considerable support to this view, and there seems to be no reason for doubting it. The divisions in the sporogenous tissue of Ophioglossum are far less regular, and this may be the cause of the irregularity in the blocking. **Beer** notes that the process in Helminthostachys is less regular than in Botrychium. It is far more regular, however, than in Ophioglossum. An exceptionally regular case is shown in *fig. 5*.

Correlated with the question of blocking is that of the division of the sporogenous cells. In Botrychium, and to a less degree in Helminthostachys, division is simultaneous in the sporogenous tissue up to the time of blocking. After the blocks become independent, the cells of each block divide simultaneously, but different blocks may develop at different rates. Even so early as the stage shown in *figs. 1* and *8*, the cells do not develop at the same rate nor do they divide simultaneously. That there is some coordination, however, is shown by the fact that figures do not usually occur isolated, but in small groups. Cells in the synapsis stage were noted in some sporangia when other cells seemed not to have reached the mother-cell stage. Oddly enough, however, most or all of the cells come out of the synapsis at about the same time. This seems to be the only point in the development at which the cells are all at approximately the same stage. Each cell seems to develop independently of the others in the majority of cases, although there are not lacking frequent cases where several cells lying side by side are approximately in the same phase. The most striking examples of this, are groups of cells in the late prophase often found among young tetrads or even in sporangia, where the young spores have become separated and have rounded off. *Fig. 9* gives a view of a mother cell in synapsis (the synaptic knot has been simplified in drawing for the sake of clearness). The cells at this stage are oblong and about $28 \times 32\ \mu$. The cell shown in the drawing is one of the largest, being $27 \times 40\ \mu$. The walls are at this time very thin and the cells have either separated from one another entirely or into small groups. The walls are so thin that it was sometimes impossible to find them, though it was always possible to find other cells younger, of the same age, and older, which showed the wall, so that it seems likely that all of them really have walls. It has already been noted that STEVENS did not find them in *B. virginianum* at certain stages. CARDIFF shows in his figures what seem to be walls, but makes no text comment. BEER is emphatic in his assertion that they are present at all stages in Helminthostachys. Recalling their exceeding thinness and the difficulty of staining them, one must accept with considerable reserve the statement that they are absent at any stage. However, when one considers that most of the walls disappear in the breaking-up of the sporogenous tissue, it does not seem altogether improbable that they may totally disappear in some cases. It may be added that the writer has been able to find them in preparations of *B. virginianum* of the same age. The preparations examined do not cover all stages, and he is therefore not able to say positively that they are always present.

The cytoplasm is very like that already described for the earlier phases of development, except that it is somewhat denser, especially around the nucleus. The synaptic knot is usually so closely massed that the course of the individual thread or threads cannot be followed for any great distance. The figure was drawn from one of the most diffuse knots in a section 10 μ thick. The chromatin seems to consist of a single row of granules strung along a continuous much tangled thread. The thread could not be determined to be continuous by direct observation, but this is made probable by the fact that there are no loose ends protruding from the knot on the uncut side. The same is true of other knots. In the early stages the thread is extraordinarily long and thin, long enough nearly to fill the nucleus with its tangled folds, and not more than 0.25–0.5 μ thick. The thread breaks up into very long slender chromosomes, which may have almost any shape from nearly straight to intricately bent and twisted.

A somewhat later stage is shown in *fig. 10,* where the chromosomes have shortened by one-half or more and have become correspondingly thicker. In the figure no attempt has been made to represent all the chromosomes in the nucleus, but only those whose shape and position could be made out clearly. The drawing was made from a section in which the knife has passed almost exactly through the center of the nucleus, and the cut side of the nucleus lies up. This gives a clearer field, but has the disadvantage that some of the chromosomes are cut in two. More than sixty chromosomes are shown in the drawing of this half-nucleus. Attempts were made to count the chromosomes at this stage, in the stage shown in the next figure, in polar views of the second division, and elsewhere, but without success. The number exceeds 100, but probably does not reach 120 for the gametophytic tissues. The chromosomes continue shortening and thickening until they reach the shape and size shown in *fig. 11.* The nuclei have their maximum size at about this stage, being 23–24 μ in diameter.

During the development of the chromosomes the wall remains thin and stains lightly, as in previous stages. The cytoplasm, however, has increased in density somewhat and has become more finely vacuolate. There appear in it about this time certain oval bodies staining very intensely with Haidenhain's iron-alum and haematoxylon, but lightly with most other stains. The staining reactions make it improbable that they are starch or chromatic material or any of the more usual constituents of cells. They are probably some sort of stored-food material, since they disappear slowly at a later stage, when such stored foods are being used. They appear in all stages following this up to about that shown in *fig. 23.* Their number and size in different cells varies greatly, in some being absent. Some of them are shown in *figs. 11–21.* They are usually much more numerous than shown in the figures, which show only those visible in a single optical focus, or even fewer than that in *figs. 17–20.* They often line up along the central region of the spindle of the first division, or along the subsequent wall (when one forms) in such masses as to obscure the details of cell structure entirely in that region. The cytoplasm itself grows denser and denser as the time of division approaches; *fig. 11* shows it at about its maximum. *Figs. 11* and *13* show two different aspects of the cytoplasm of dividing cells, the former being the common one. The beaded threads shown in *fig. 12* are very characteristic of the cytoplasm of the cells during maiosis.

The spindle originates as a weft of kinoplasmic fibers around the nucleus. The fibers then form a number of poles such as those shown in *fig. 11.* Three of these poles become prominent and the others disappear. The tripolar stage passes into the bipolar by the further elongation of two poles and the breaking-up of the third (*fig. 12*). *Fig. 13* presents a surface view of the mature, sharply pointed, bipolar spindle. The chromatic mass (simplified in the figure) proved too dense and the chromosomes too small and numerous to make any trustworthy observations on the method of chromosome splitting. The chromosomes usually pass to the poles in a more or less straggling manner, though sometimes they advance in regular lines. Reaching the poles they may or may not organize a resting nucleus; when the second division follows very soon they probably do not. *Fig. 14* shows the beginning of the formation of the resting network before the spindle has disappeared. *Fig. 15* shows the chromosomes still free after the formation of a wall between the daughter nuclei. In *fig. 16,* from which the spindle fibers have not entirely vanished, the daughter nuclei are in the resting condition.

After the first division, a wall may (*figs. 15, 16, 19, 20*) or may not (*figs. 14, 17, 18, 21*) form before the next division. Probably this depends on the rapidity with which the second division follows the first, and perhaps the usual thing is for the second division to occur when the daughter nuclei have reached about the stage shown in *fig. 14*. At this time the chromosomes usually have not formed a resting network, and the central part of the first spindle still persists. If division occurs at this stage, the resulting figure usually resembles *figs. 17* and *21*. The majority of the spores are of the tetrahedral type. In this region of the cell, whether the wall forms or not, there is always a noticeable collection of fine granular cytoplasm which is sharply distinguishable from the less dense parts containing the beaded strands already mentioned. Within this zone most or all of the food granules are found; they are often so numerous and so densely crowded as to make it difficult or impossible to tell whether a wall is present or not.

Early stages in the development of the spindle of the second division were not observed. Metaphases are shown in *figs. 17* and *18*, and anaphases in *figs. 19* and *20*. All the spindles with the exception of the type shown in *fig. 18* are sharply bipolar, though somewhat blunter than those of the first division. The spindle fibers are markedly different from those of the first division; instead of a loose bundle of very fine fibers, the fibers are heavy and coarsely beaded. All the spindles arranged as in *fig. 18* have their apices truncated. *Fig. 19* shows one spindle in the linear position, the other not; in this type no truncated spindles were observed. *Fig. 20* shows the bilateral arrangement; no other figure with this arrangement was observed, though one case of bilateral spores was noted (*fig. 25*). *Figs. 17–20* are arranged in the order of frequency of their occurrence in the preparations. No spores were found which could be referred to the types of division shown in *figs. 18* and *19*, which is singular, considering the frequency of this type of arrangement at time of division; they were probably present, but were not recognized. In *fig. 20* the chromosomes seem to be passing into the network characteristic of resting nuclei even before reaching the poles of the spindle, and long before any nuclear membrane has formed.

During maiosis the wall of the mother cell still persists and is very noticeable, owing to its separation from the contents, for which it seems ordinarily to be far too large. Such a wall, in contact with the contents at one point only, is shown in *fig. 15*. This wall persists around the tetrad until late in the development of the spores. The wall with its contents lies in a vacuole of the tapetal cytoplasm. The vacuole is limited by a plasmatic membrane often more prominent than the wall of the mother cell within it. Where the two are in contact they are distinct, showing that the vacuole is a real one and is not merely the effect of shrinkage in preparing the material. I was not able to determine just how long the old wall persists, but it was found (at least parts of it) around spores as old as those shown in *fig. 27*.

The beginning of the tetrad walls is shown in *fig. 21* and the completed wall in *fig. 22*. It is formed partly on the primary division spindles of the second division and partly on secondary spindle-like structures which arise between the nuclei which are not sisters. Of the six walls which meet in the middle and separate the young spores, two form on the primary spindles and four on the secondary ones. At the same time a wall forms on the outer or convex side of the spores. Whether this wall joins directly to the tetrad wall or continues around inside of it could not be determined. BEER describes this tetrad wall as uniting with the wall which surrounds the tetrad, thus forming a structure with four compartments, each of which contains a spore. It is certain that it does not do so in Ophioglossum, owing to the fact that the mother-cell wall is not at that time in contact with the spores.

The cytoplasm of the young spores is dense and granular. The resting nucleus has a rather coarse network, with the chromatin scattered over it in rather large masses (*fig. 22*). As the spores grow older they break apart, the walls thicken, and the cytoplasm becomes vacuolate. The progressive vacuolation of the cytoplasm seems to be connected with the corresponding rapid thickening of the young spore coats. The relation between the two is brought out in *figs. 22–26*. During this period of thickening of the spore walls the cytoplasm of the tapetal plasmodium also becomes more vacuolate. A decrease of its starch accompanies *pari passu* the vacuolation of the plasmodium. The degree of the collapsing action of the killing and fixing agents on the young spores affords a graphic though not very accurate means of estimating the decreasing density of their cytoplasm. At about the time the spore coats attain a sufficient rigidity to resist collapse, the cytoplasm begins to increase in density (*fig. 27*). Soon afterward (*fig. 28*) starch makes its appearance in the spore. About the same time the spore coat can be seen to consist of an exospore and an endospore. As the spore becomes older the two regions of the wall become more distinct and the exospore increases considerably in thickness. In the mature spore there are two cytoplasmic zones, an outer less dense one and an inner dense one filled with starch.

Whether the endospore originates as a separate membrane or whether it is merely the inner part of an originally homogeneous membrane which has differentiated into two could not be determined in Ophioglossum. Appearances, however, favor the latter view. Perhaps the strongest evidence in its favor is the fact that though the endospore is less distinct when first distinguishable, it is just as thick or even thicker than in the mature spore. Somewhat various opinions have been held concerning the exact method of exospore formation. DEBARY (**'64**) states that the exospore of certain Ascomycetes is laid down from the epiplasm, which might be thought to correspond roughly with the tapetal plasmodium in respect to the part either might play in the formation of the outer coat of the spore. The fact that the entire tetrad is surrounded for a considerable time by the persistent mother-cell wall, and that the whole lies in a vacuole, would seem to render this hypothesis untenable in respect to Ophioglossum. FITTING(**:00**), BEER (**:04**), and others maintain that the exospore, even though separated from the endospore and the protoplast by a space containing no protoplasm, can be built up by its activities. Miss LYON (**:05**) has shown that the two coats in Selaginella are formed by the differentiation of a single thick homogeneous gelatinous membrane. The exospore according to this view is simply the outer part in which has been deposited dense granular material; the roughness is due to the irregular way in which the material is deposited; and the endospore is the part in which no such deposits are made. This explanation seems to harmonize with the facts in Ophioglossum. Miss LYON points out that the membranes of Selaginella are not separated and suggests that where they seem so it is due to action of the reagents used in preparing the material. There is

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no separation in Ophioglossum, and in consequence no necessity for action at a distance greater than the thickness of the spore coat. The supposed semi-fluid character of the membrane at the time of its formation would reduce this difficulty to a minimum.

Interesting irregularities occur in the development of the sporogenous tissue. It has already been pointed out that the mother cells may develop at very different rates. *Fig. 11*, for example, was drawn from a sporangium containing young tetrads and various stages of the first and second divisions. Still more interesting irregularities are shown in *figs. 30–33*. *Fig. 30* shows an enlarged mother cell in the metaphase of the first division; it was found among spores slightly younger than the one shown in *fig. 27*, and its wall is indistinguishable from those of the spores among which it lies. This figure afforded the best opportunity observed for obtaining an approximate count of the chromosomes. Owing to the way in which they are scattered, most of them are sufficiently free from their neighbors to be identified and counted; 102 are shown in the drawing, which represents about one-half the entire figure. About as many more could be counted in the sections adjacent to this on each side, thus making the gametophyte number somewhat over 100. *Fig. 33* shows three spores within a common exospore, one of which is plainly degenerating; no trace of the fourth member of the tetrad could be found. Such a structure could arise from the one just discussed by the division of one of the daughter nuclei and each of the three resulting nuclei and its accompanying cytoplasm surrounding itself with a wall. *Fig. 31* shows a body consisting of eight cells, with thin outer wall and very delicate division walls. The cytoplasm is dense, finely reticulated, and crowded with starch, which is also abundant in the tapetal plasmodium around it, though not found in the young spores in the same sporangium nor in any spores until they are much nearer maturity. This might suggest that the normal young spores are poor in cytoplasm and stored food because they use it to build their rapidly thickening walls. Though varying in size the nuclei are all large, being about the size of the entire young spores in the same sporangium. With Flemming's triple stain they stain uniformly with the gentian. *Fig. 32* represents another structure of the same sort but with twenty nuclei, two of which are very large. These bodies have probably arisen from the germination of the members of a tetrad which failed to separate in the usual way. Possibly the lack of a thick wall around the young tetrad is responsible for the continued growth; at any rate, no indication of the germination of ordinary thick-walled spores was observed, unless *fig. 30* be interpreted as such. Not unlike this is the production of more than four microspores in some angiosperms, but so far as I am aware similar phenomena have been reported in only one homosporous plant. In an account of the germination of the oospore of Coleochaete, Allen shows that reduction takes place with the first division; the spores thus produced germinate and cooperate to produce a multicellular mass of gametophytic tissue. Each cell of this mass of tissue eventually produces a zoospore which gives rise to the ordinary vegetative phase of the plant. Wille has shown (**'86**) that in certain angiosperms by a suppression of the second maiotic division a mother cell may give rise to two microspores only instead of the usual four. Since in at least the majority of plants the unlike elements of the bivalent chromosomes are separated in the first division of the mother cell, there seems to the writer no valid reason, other than that imposed by the available food supply and the ordinarily thick walls, why any number of spores more than two may not arise from a mother cell. In a discussion of many-spored asci Overton (**:06**) has recently shown that the number of divisions in the ascus is immaterial so far as the essential nature of the resulting spores is concerned. In this connection the recent experimental work of Němec (**:06**) is of considerable interest; by subjecting staminate flowers to the action of chloroform vapor he secured pathological conditions closely paralleling those herein described. His attempts to germinate these bodies should yield interesting results.

SUMMARY AND COMPARISON

The following tabular form of statement will serve to contrast compactly the three genera of Ophioglossales as to their sporangia.

Ophioglossum	*Helminthostachys*	*Botrychium*
1. Outer wall and corresponding parts of the tapetum and the sporogenous tissue from one or two superficial cells of a sporangi-	The essential parts from a single superficial cell.	Like preceding but smaller contribution of neighboring cells.

Ophioglossum	*Helminthostachys*	*Botrychium*
ogenic band; remainder of sporangium formed by the cells of the adjacent sterile tissue.		
2. Freely exposed outer wall 5-layered and from primary wall cell (or cells).	Similar to the preceding in origin and development, except that in most species the entire wall so arises.	Like preceding but still further restricted to a single cell in origin.
3. Sporangia sunken.	Sporangia intermediate.	Sporangia generally short-stalked.
4. Dehiscence by transverse slit.	By longitudinal slit.	By transverse slit.
5. One to three primary sporogenous cells.	One primary sporogenous cell.	One primary sporogenous cell.
6. Tapetum unusually two-layered and its cells tangentially elongated.	Cells radially elongated, otherwise like preceding.	Same as preceding except that there are two to four layers of radially elongated cells.
7. Nuclei of tapetal plasmodium probably do not increase in number.	Amitosis of these nuclei probably occurs.	Amitosis usual and frequent.
8. Nuclei of plasmodium do not increase in size.	No increase in size.	Nuclei increase to four times their original size.
9. Tapetal nuclei persist up to near time of dehiscence.	More persistent than in preceding.	Less persistent than other genera.
10. Sporogenous tissue separates into irregular masses.	Blocking much more regular.	Blocking extremely regular.
11. Division of sporogenous tissue up to mother cells not wholly simultaneous.		Simultaneous division the rule.
12. Maiosis in different mother cells varies widely in time and in arrangement of spindles.	Maiosis in each mother-cell independent.	Division simultaneous in each block of cells.
13. Spindle extra-nuclear.		Spindle intra-nuclear.
14. Chromosomes 100 to 120 after reduction.	Reduced number 40 to 60.	No data.
15. Spindles in all possible positions with reference to one another.		"Either in same plane or perpendicular to one another."

Ophioglossum	*Helminthostachys*	*Botrychium*
16. Wall formed or not after first maiotic division.	Special tetrad wall incloses each spore in a separate compartment.	No wall formed.
17. Tetrads for a long time inclosed within persistent mother-cell wall.		Tetrad inclosed within persistent wall of mother cell.

The features common to the genera are: (1) the breaking-down of the inner layers of the wall, (2) the penetration of a plasmodium, derived from the tapetal cells, among the sporogenous cells, (3) the failure of the mother cells to contribute to the tapetal plasmodium, (4) the formation of a resting nucleus after the first maiotic division, (5) the appearance in the spore-plasm of a phase of decreasing density followed by one of increasing density, the former possibly connected with the rapid growth of the young spore coat (no data from Botrychium), (6) the spores rich in starch, (7) the tetrads in vacuoles of the plasmodium.

This investigation was carried on under the direction of Professor John M. Coulter and Professor Charles J. Chamberlain.

The University of Chicago

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EXPLANATION OF PLATES III AND IV

All figures were drawn with the aid of a Bausch and Lomb camera and Zeiss apochromatic objectives and compensating oculars, and reduced one-half. *Figs. 1–7* and *fig. 32* were drawn under a low-power dry lens, the others under 1.5^{mm} immersion.

PLATE III

FIG. 1. Wall of three or four layers; last wall formed indicated by *1;* tapetum one-layered except at left. ×300.

FIG. 2. Wall four- or five-layered; tapetum two-layered; sporogenous tissue beginning to break up into irregular blocks and to separate from the tapetum. ×300.

FIG. 3. General view of about one-half of a sporangium, showing four or five layers in the wall; two-layered tapetum; sporogenous tissue broken up into irregular blocks; the regular two-layered tapetum is restricted to the left of the figure; in the remaining part it is difficult to distinguish it from the sporogenous tissue; *1* is last wall formed. ×123.

FIG. 4. Tapetal plasmodium penetrating among blocks of sporogenous tissue; tapetal nuclei mainly around periphery; blocks of sporogenous tissue quite irregular. ×300.

FIG. 5. An unusually thick tapetum and more regular blocks of sporogenous cells, somewhat older than those of *fig. 4*. ×300.

FIG. 6. Longitudinal section of wall; tetrad stage of sporogenous tissue; to show early indications of formation of slit for dehiscence. ×300.

FIG. 7. Mature wall showing longitudinal section through line of dehiscence; inner cell layers broken down. ×123.

FIG. 8. A sporogenous cell lacking about two divisions of the mother cell; from sporangium with a three-layered wall. ×900.

FIG. 9. Synapsis of mother cell; synaptic knot has been simplified in drawing for the sake of clearness. ×900.

FIG. 10. Prophase of first division; chromosomes about one-half the length of their earliest stage; food granules in cytoplasm. ×1200.

FIG. 11. Origin of spindle; chromosomes in mature form, many of them seem paired; food granules in cytoplasm; cell appears small because it is not drawn in median optical section. ×900.

FIG. 12. Spindle passing from tripolar to the bipolar stage; food granules and beaded kinoplasmic threads prominent. ×900.

FIG. 13. Surface view of mature spindle at metaphase; cytoplasm unusually free from food granules and kinoplasmic threads. ×900.

FIG. 14. Telophase of first division; nuclear membrane formed and chromosomes mostly free from one another; middle region of cell occupied by persistent spindle fibers, food granules, and denser cytoplasm; old wall becoming freed from contents. ×900.

FIG. 15. Later telophase; a wall has formed, along which the food granules tend to line up; mother-cell wall almost entirely free from contents; chromosomes quite free from one another. ×900.

FIG. 16. Part of tapetal plasmodium containing much starch; tapetal nuclei show the aggregation of chromatic material into elongated masses, far fewer than the chromosomes; mother cell after first division, with a wall and daughter nuclei in resting condition; the whole lies in a vacuole of the plasmodium; old mother-cell wall surrounds it, but is not in contact with it and is not shown in the drawing. ×900.

PLATE IV

FIG. 17. Usual position of spindle with no wall between, will result in tetrahedral arrangement of spores; note difference between first and second spindles; many chromosomes left out for clearness. ×900.

FIG. 18. Linear arrangement of spindle; spindle fibers do not come to a point; as in all cases, granular cytoplasm and food granules collect in middle region, whether a wall is present or not. ×900.

FIG. 19. Combination of linear and bilateral arrangement; linear spindle pointed, though this was never observed where both spindles are placed linearly; a wall in this and next figure. ×900.

FIG. 20. Bilateral arrangement of spore nuclei; chromosomes already fusing before reaching the poles. ×900.

FIG. 21. Telophase and earliest indication of tetrad walls. ×900.

FIG. 22. Young tetrad with dense cytoplasm and thin wall. ×900.

FIGS. 23, 24. Progressive vacuolation of spore-plasm and correlated thickening of spore wall. ×900.

FIG. 25. Depletion of tapetal plasmodium and increase of its vacuoles; bilateral spores shown within vacuole. ×900.

FIG. 26. Maximum depletion of spore-plasm; spore walls rather thick and probably gelatinous, collapsing under the action of the reagents. ×900.

FIG. 27. Spore wall rigid enough to resist collapsing action of reagents; wall beginning to be slightly denser and rougher. ×900.

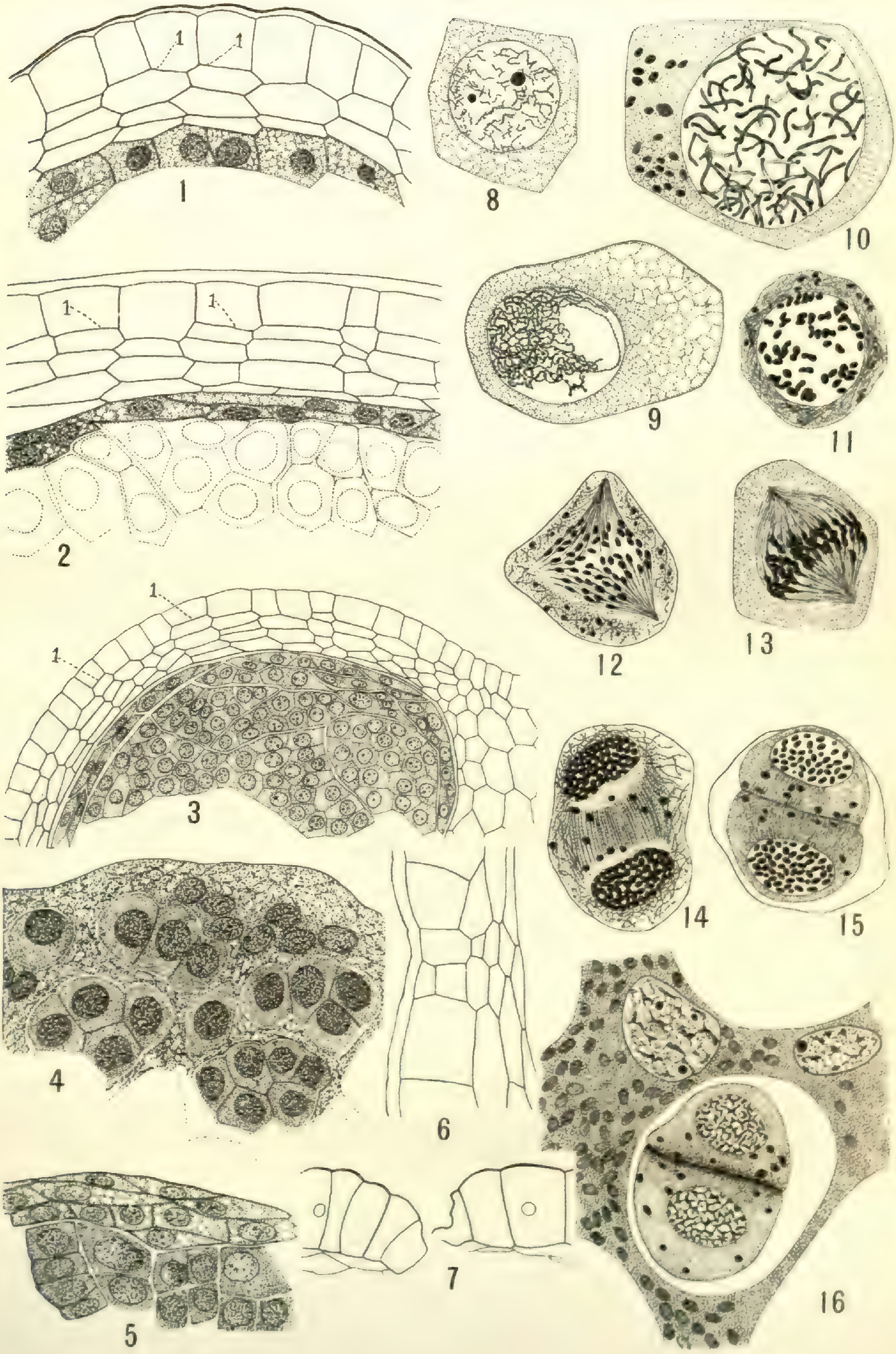
FIG. 28. Spore coat distinctly differentiated into two layers; the cytoplasm much denser and showing very small starch grains. ×900.

FIG. 29. Mature spore with thick wall and abundant contents; starch very abundant; intine penetrates exine at tip of spore. ×900.

FIG. 30. Much delayed division of a mother cell, spore-coat-like wall surrounding it. ×800.

FIGS. 31, 32. Multicellular gametophytic (presumably) masses of cells, which have arisen through the cooperative germination of the members of a tetrad which failed to separate in the ordinary way. ×233.

FIG. 33. Three of the four spores of a tetrad within a common exospore. ×600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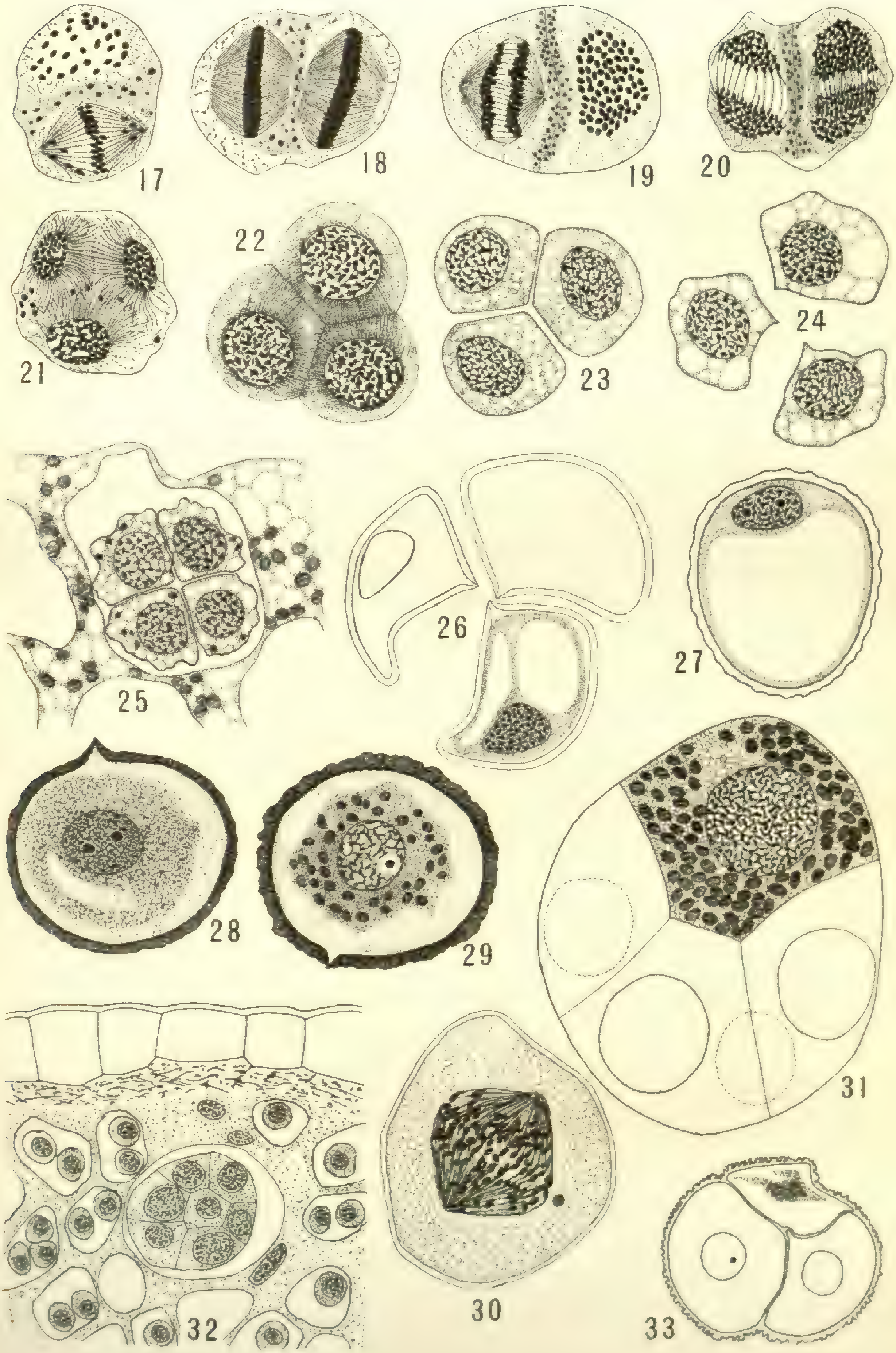
BURLINGAME on OPHIOGLOSSALES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BURLINGAME on OPHIOGLOSSALES

THE ROOTS OF LYCOPODIUM PITHYOIDES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCV

ALMA G. STOKEY

(WITH PLATES V AND VI AND ONE FIGURE)

Lycopodium pithyoides Schlecht. & Chamisso is a subtropical form of rare occurrence, but, according to UNDERWOOD and LLOYD, of unexpectedly wide distribution. In spite of its striking and unmistakable appearance, it has been confused with other forms, such as *L. dichotomum*.

The material which formed the basis of this investigation was collected in September 1906 near Jalapa, Mexico, by Professor BARNES, Dr. CHAMBERLAIN, and Dr. LAND, of the University of Chicago. They found in that region only one specimen, which they secured and which is now growing in the greenhouse of the University. This plant, or rather clump of plants, was growing as an epiphyte on the trunk of a recently fallen tree.

This species of Lycopodium attains a size unusual in the genus. The stem is dichotomously branched, erect, and rigid, with a diameter of 6 to 10^{mm}; and the slender dark green leaves are 2.5 to 3.5^{cm} long. The fact that practically every leaf is a sporophyll indicates that this form is of relatively primitive character. The length of its leaves, the stoutness and rigidity of its stem, and its unusual size give it such a shrub-like aspect that SCHLECTENDAL and CHAMISSO (**10**) in the original description very aptly compared it to a young *Pinus silvestris*.

A cross-section of the stem, however, is much more striking than the general habit. The stele, which in structure and arrangement is similar to that of *L. lucidulum* or *L. Selago* is comparatively small, being about one-tenth the diameter of the stem. The conspicuous feature of the stem is not the central stele, but the numerous smaller heavily sheathed steles which surround it (*fig. 1*). These are the "inner roots" of STRASBURGER (**11**). The "inner root" is not an example of a particular type of root, but of a peculiar habit which exists in certain species of Lycopodium. The roots arise in acropetal succession at any point of the stele of the stem. Instead of penetrating the cortex at once and emerging as aerial roots, they turn down in the cortex, boring canals through long stretches of cortex, and emerge finally at or near the base. This habit is associated with erect forms of Lycopodium, both terrestrial and epiphytic. A similar habit is described in the Marattiaceae, SACHS (9) having given a brief description of its occurrence in *Angiopteris evecta*, in which the roots are said to bear a definite relation to the leaf bases.

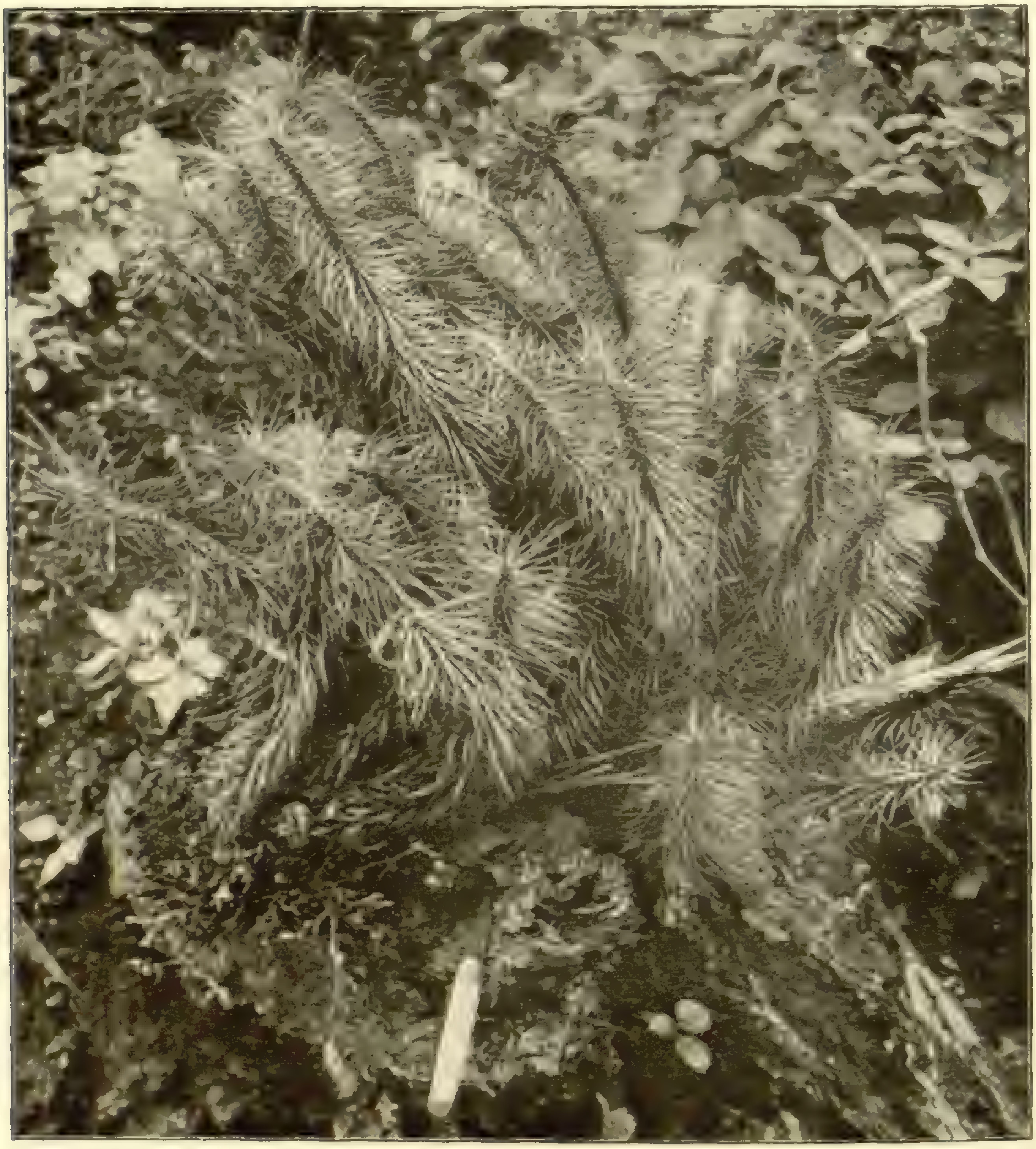

FIG 1 —Lycopodium pithyoides

The "inner roots" of Lycopodium were described by BRONGNIART (**1**), who stated that they were characteristic of erect dichotomous forms. STRASBURGER (**11**) described the more obvious features of the "inner roots" of *L. Selago*, and gave a list of about twenty species characterized by their presence. All the species noted are members of the Selago group except *L. Phlegmaria*. In none of the species described have the "inner roots" attained a development comparable to that in *L. pithyoides*. Few have been studied in sufficient detail to afford a basis for comparison. STRASBURGER records *L. Selago* as showing eight roots in a cross-section taken 5^{cm} above the base of the stem. BRONGNIART (**2**) figures *L. phlegmaria* and *L. verticillatum* with fifteen "inner roots." *Fig. 2* shows a cross-section of *L. pithyoides*, taken $10–12^{cm}$ above the base of the stem, in which fifty-two roots were found. The extraordinary development of these roots is no doubt an important factor in giving the stem its characteristic stoutness and rigidity.

The root primordia usually appear within $2–5^{mm}$ of the tip of the stem, but occasionally there will be none within $5–10^{cm}$ of the tip. The primordium shown in *fig. 3* and *fig. 4* was found about 2^{mm} from the apex of a stem which was about 25^{cm} high. The vascular cylinder of the stem was still in the promeristem stage.

The roots of *L. pithyoides* show four distinct initial regions for the plerome, periblem, dermatogen, and calyptrogen. The plerome arises from an initial region consisting probably of only one initial cell. It was impossible to determine with certainty the exact number of initials, but such preparations as that shown in *fig. 5* indicate a single initial; it is possible, however, that there are several, as in the forms studied by BRUCHMANN (**3**). The periblem initial region consists of several layers forming a well-defined although not sharply differentiated region. There is a well-defined one-layered dermatogen which gives rise to the epidermal cells and trichoblasts.

The trichomes arise from definite cells which are cut off by curved oblique walls from the original epidermal cells a short distance back of the apex of the root (*figs. 6, 7, 8*). With the growth of the epidermal cells and trichoblasts, the latter come to have the appearance of wedge-shaped cells. The outer wall rounds out and a papilla appears which rapidly elongates into a slender, rather thick-walled, persistent trichome. The trichoblast usually divides once longitudinally, so that the trichomes are usually found in pairs (*fig. 9*). Since almost every epidermal cell gives rise to a trichoblast, the trichomes are abundant and very uniformly distributed. The trichoblastic cells are cut off as regularly in the "inner roots" as in the external, but of course produce trichomes only in aerial and soil roots. The formation of trichoblasts in Lycopodium was first described by NAEGELI and LEITGEB (6). LEAVITT (5) has described them in greater detail, giving *L. inundatum* as an example of the type in which the trichome is cut off by a straight anticlinal wall, and *L. lucidulum* as an example of the type with oblique walls. The development of the trichomes in *L. pithyoides* seems to be the same as that in *L. lucidulum.*

The root begins to grow downward immediately after leaving the stele (*fig. 10*), dissolving and crushing the cortex to make way for its rapid enlargement. The roots bend and curve, winding in and out around each other and around the leaf traces as they work their way down the stem. Several roots often run side by side for a considerable distance, so crowded together that the sheaths appear to fuse. PRITZEL (7) and STRASBURGER both describe branching as of frequent occurrence. It must be extremely rare in *L. pithyoides,* for no cross-sections have revealed the slightest trace of it, and an extensive dissection of the stem was equally unsuccessful. That it does occur is shown by a root-tip taken from an "inner root" which has the dichotomous forking so characteristic and abundant in external roots (*fig. 11*). It is possible that in such cases one branch may become abortive owing to the crowded condition under which the root is growing.

A typical "inner root" is shown in *fig. 12.* On the outside is a heavy sclerenchyma sheath, which in some roots attains a thickness two or three times as great. Within the sheath is a region of slightly thickened parenchyma which extends to the stele. The parenchyma region is the one which STRASBURGER erroneously called the outermost region of the root, because of the ease with which it is separated from the adjoining sclerenchyma. BRUCHMANN (4) in his discussion of *L. Selago* corrected this error. The tearing between the two regions is due not to a lack of organic connection, but to the weakness of the middle lamella of the inner cells. It is so delicate that any pressure sufficient to section the sclerenchyma sheath is almost certain to cause a splitting of the middle lamella. Although the two regions are rather sharply defined, there are always a few cells in the transition stage. The thin-walled cortex is limited by the endodermis, which although not sharply differentiated can be easily recognized by its suberized walls.

In the genus Lycopodium there is great variation in the type of stele found in the root. RUSSOW (**8**) has described that of *L. annotinum* and *L. complanatum* as being almost identical with that of the stem, but the stele of *L. Selago* and *L. inundatum* as being strikingly different. *L. pithyoides* is similar to *L. Selago.* The vascular strand is collateral, with a crescent-shaped xylem, the phloem lying between the horns of the crescent. The protoxylem is found regularly occupying the horns, but occasionally it spreads along the outer region of the metaxylem. There is no evident differentiation into protophloem and metaphloem either in root or stem. RUSSOW in his discussion of *L. Selago* regards the parenchyma region outside the xylem as belonging to the phloem, and consequently classes the bundle as concentric. This indefinite region may be one or two cells thick or may be altogether lacking, and it seems better to regard it as pericycle rather than as phloem. It consists of small thin-walled parenchyma cells containing protoplasm and nuclei, with none of the wide-mouthed thick-walled cells which characterize the phloem region. The shape of the xylem strand varies somewhat in different parts of the root. The origin from the stele is seen in *figs. 13* and *14.* It is connected with two of the xylem strands and one of the phloem; this arrangement is shown in the primordium stage shown in *fig. 4.* As the root leaves the stele of the stem, the xylem strands move together, forming a U-shaped figure, with the closed end toward the center of the stem (*figs. 15* and *16.*) As the root passes down the stem, the xylem becomes massed together, so that when the root leaves the stem it has the form shown in *fig. 17,* which is the arrangement characteristic of external roots. The behavior of the xylem during forking of the root is shown in *figs. 18, 19, 20.* The xylem divides at the place where the two strands had previously united, and each strand rapidly assumes the characteristic crescent-shaped form.

The region of exit of the roots extends from the base of the stem to about 1^{cm} above. BRUCHMANN (3) found that in *L. Selago*, when the stem was closely appressed to the ground, an earlier exit was favored. The root may bend abruptly and leave the stem at a right angle, or it may run around the stem for a short distance not far below the epidermis, leaving the stem at a tangent; but it is more usual for the root to turn gradually toward the outside of the stem and leave it obliquely. The root hairs which in the "inner roots" develop no further than the trichoblast stage, develop extensively and form a dense mat around the external root (*fig. 21*). The epidermis, which soon disappears in the "inner root," is persistent in the external. In an old stem in which the departing roots are numerous and thickly crowded, the cortical tissue of the stem becomes torn and fragmentary. Most of it disappears, leaving a brush-like mass of roots with very little cortex between them.

This investigation was conducted at the University of Chicago under the direction of Professor JOHN M. COULTER and Dr. W. J. G. LAND, and arose incidentally in connection with an investigation of the development of the stele of Lycopodium.

THE UNIVERSITY OF CHICAGO

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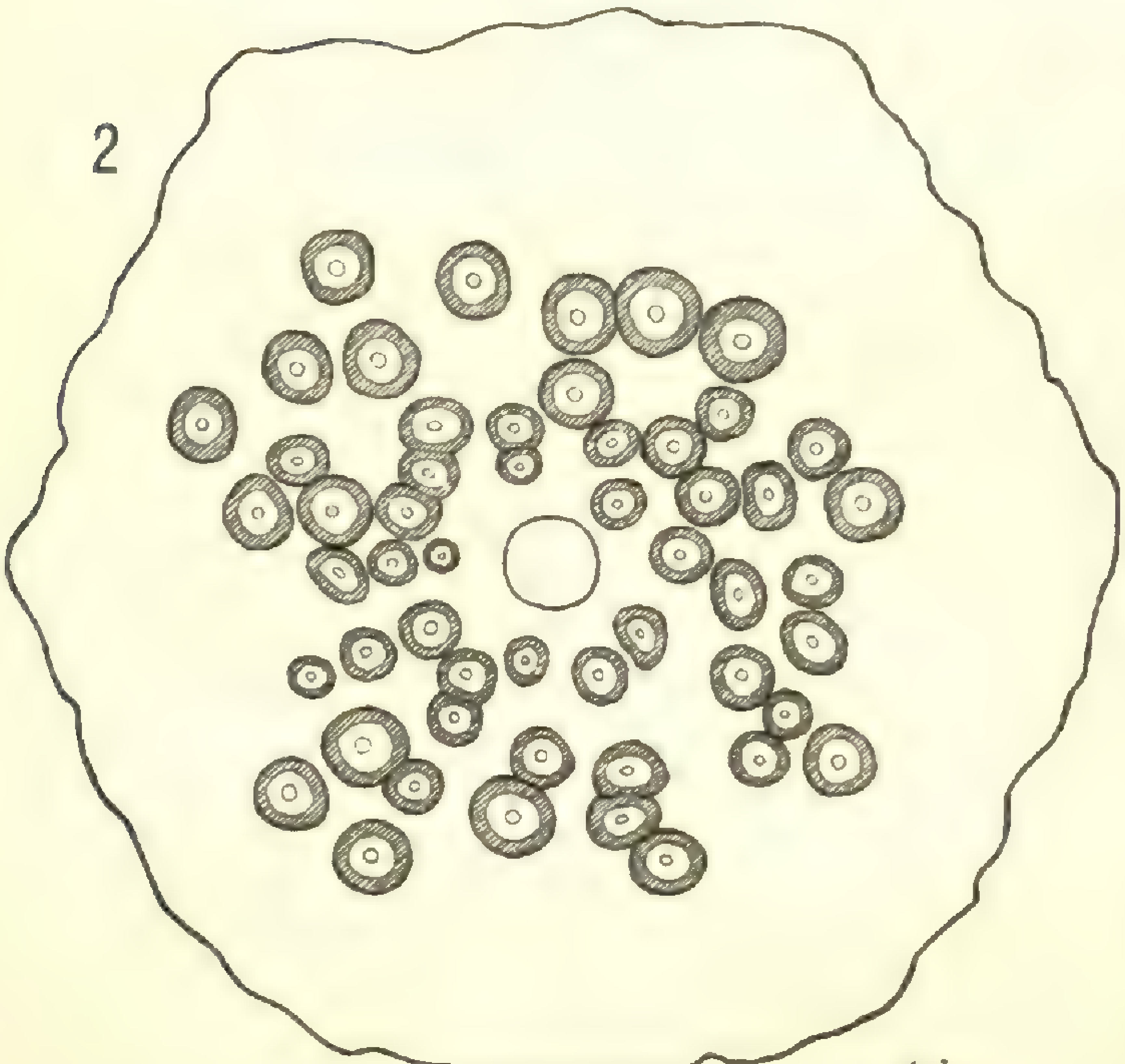

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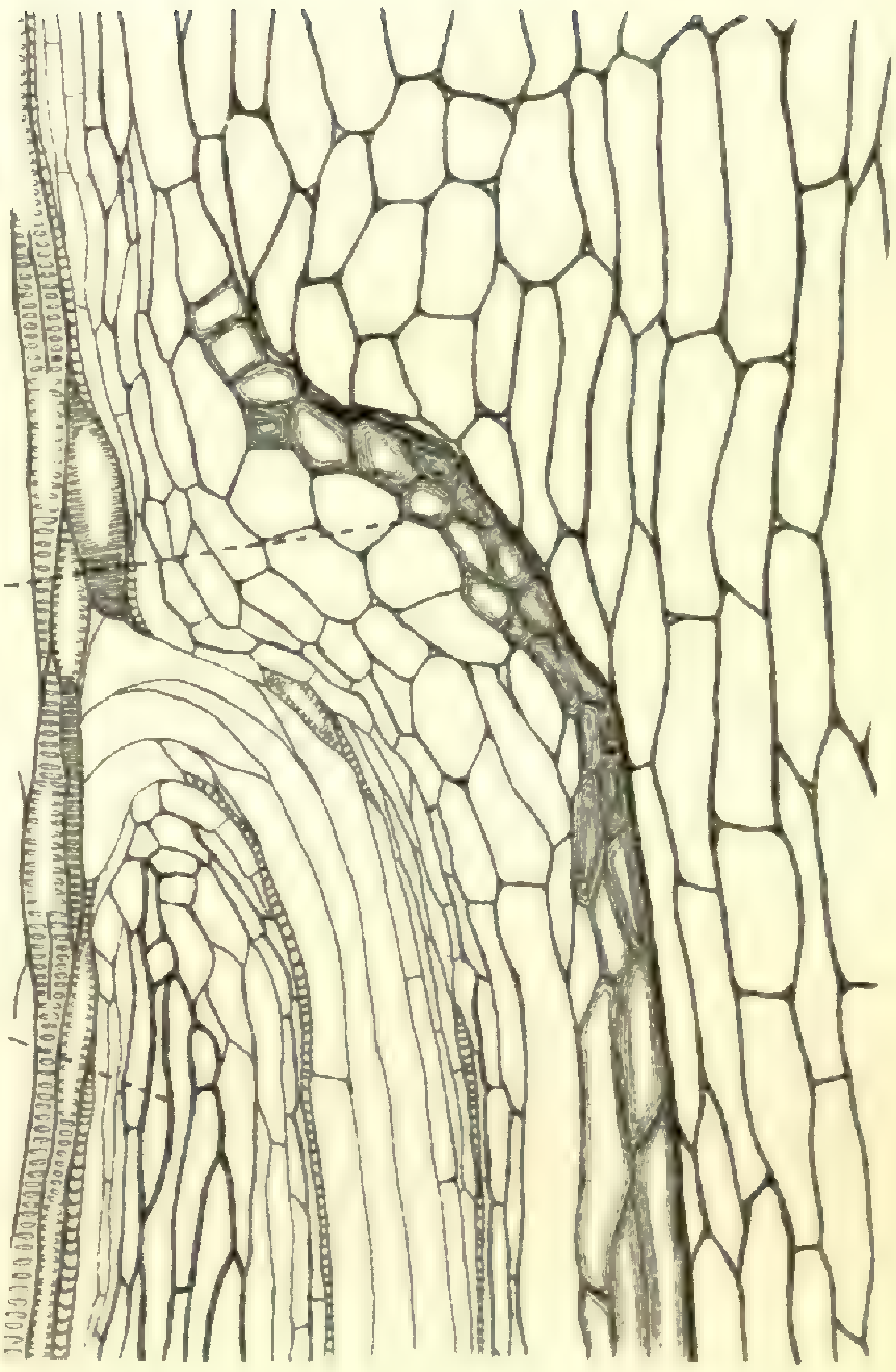

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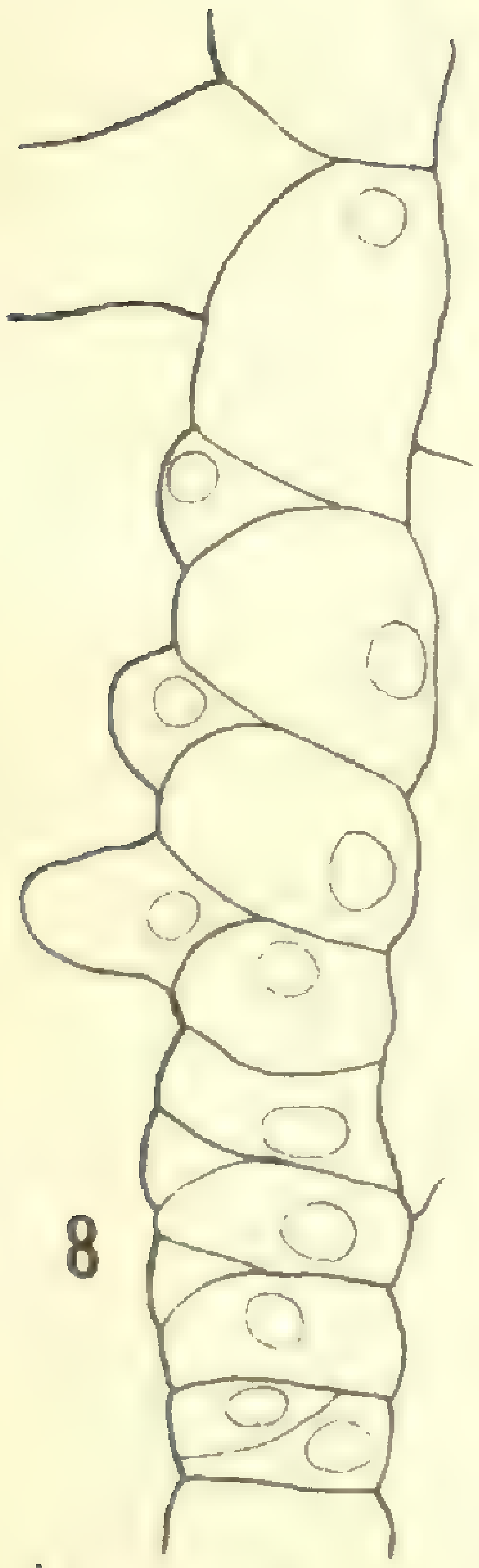

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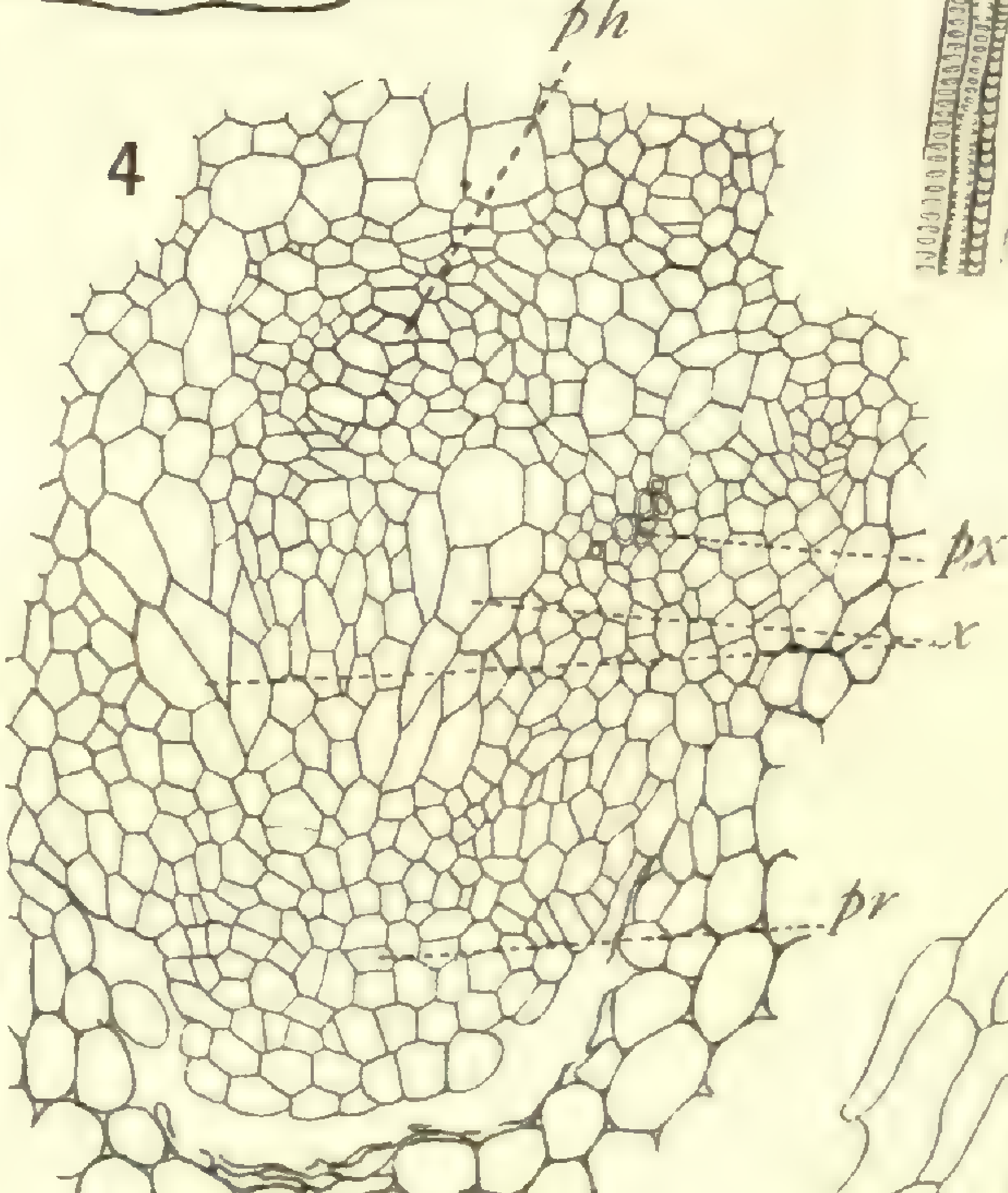

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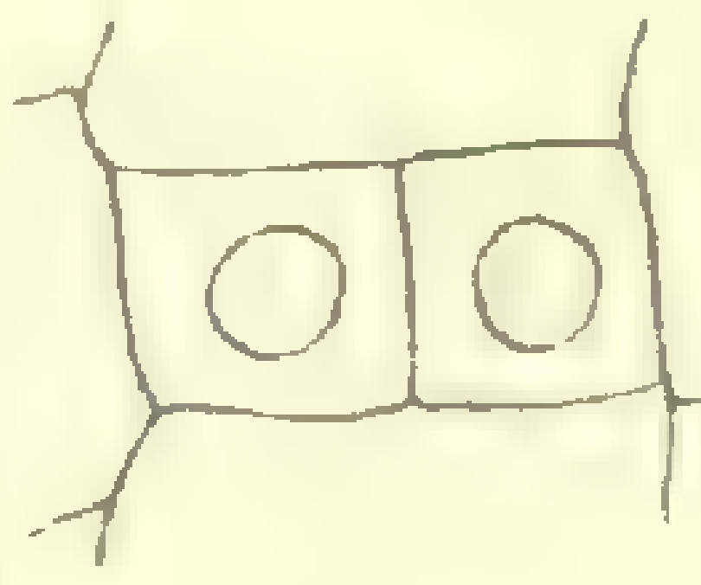

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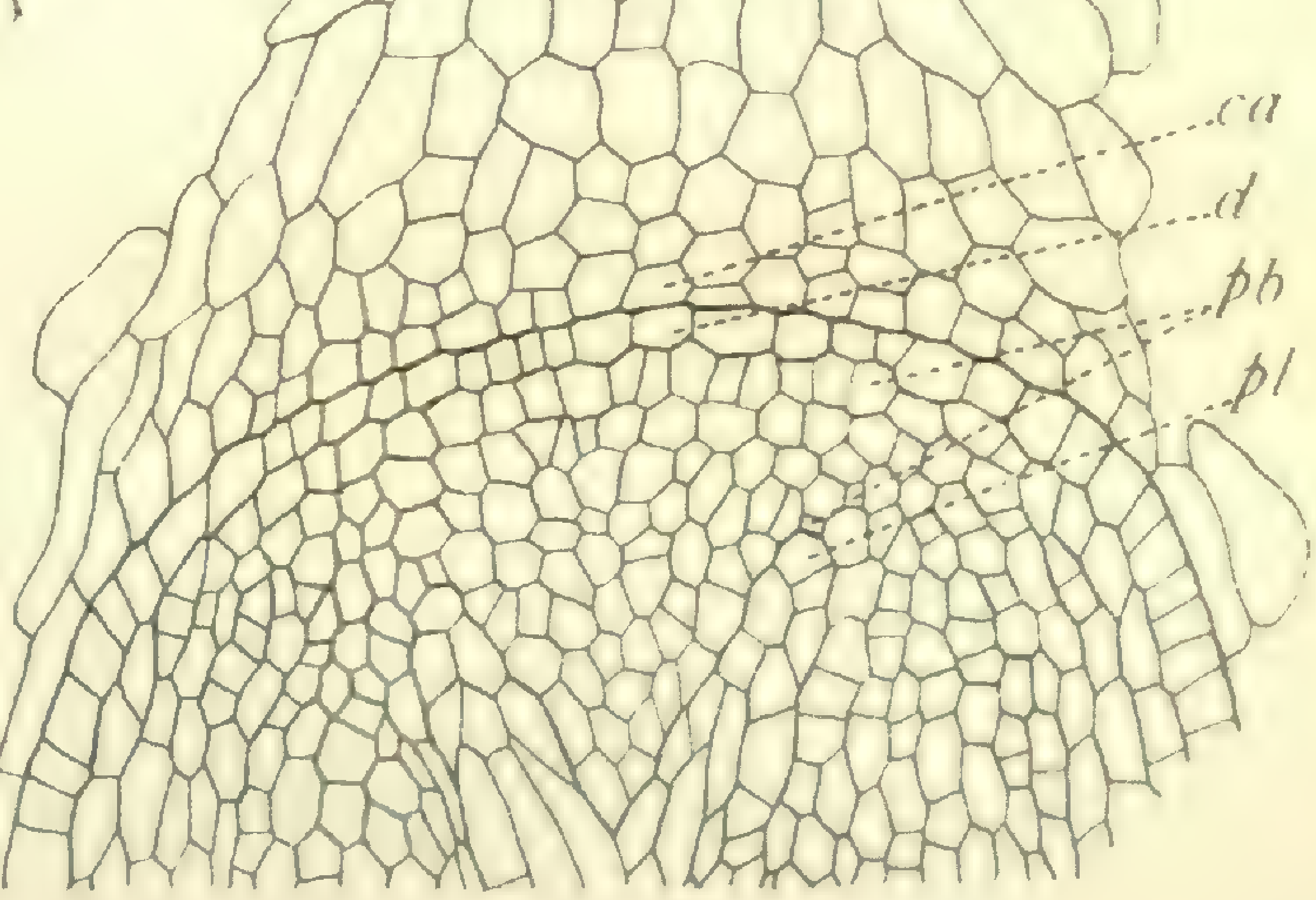

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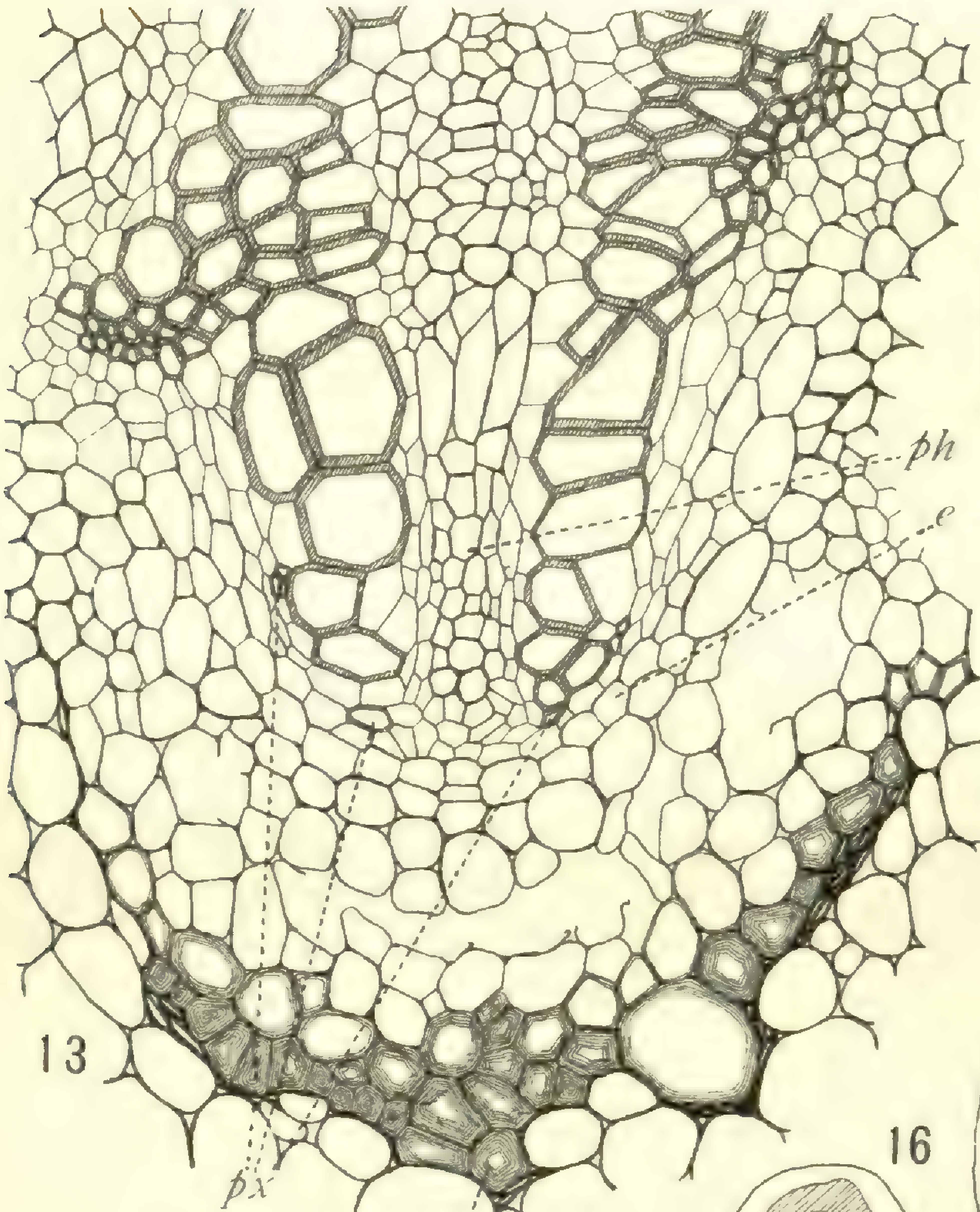
STOKEY on LYCOPODIUM



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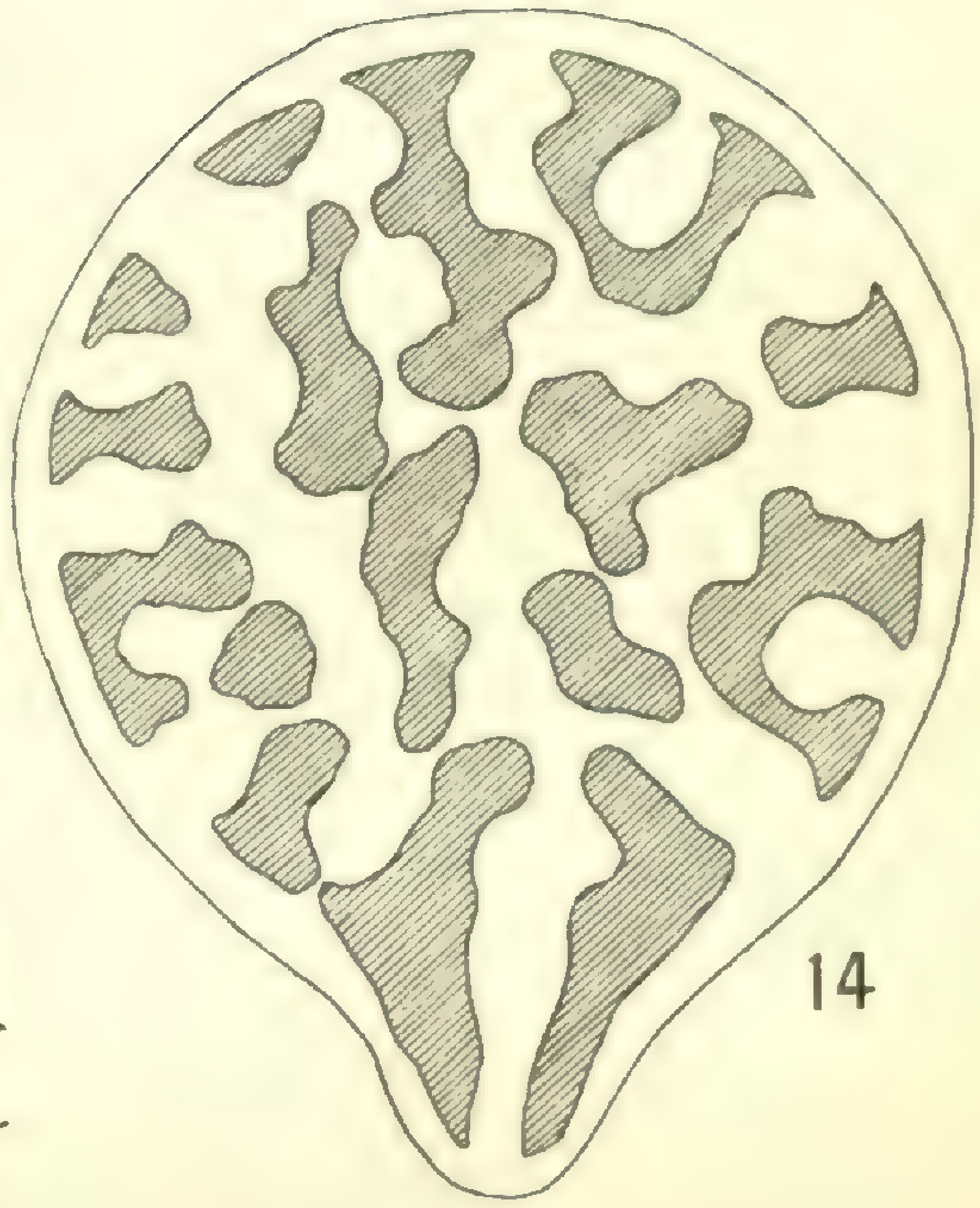

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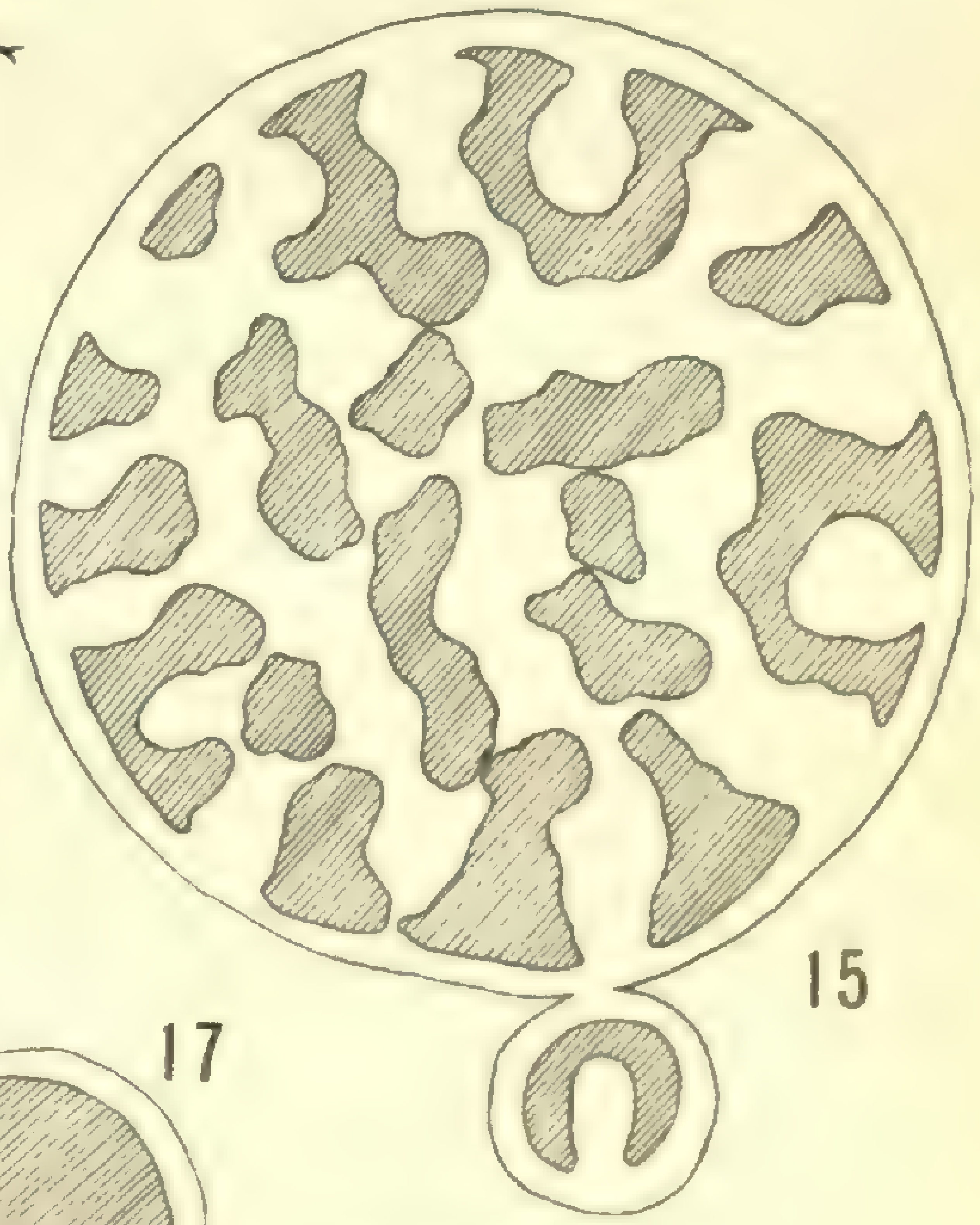

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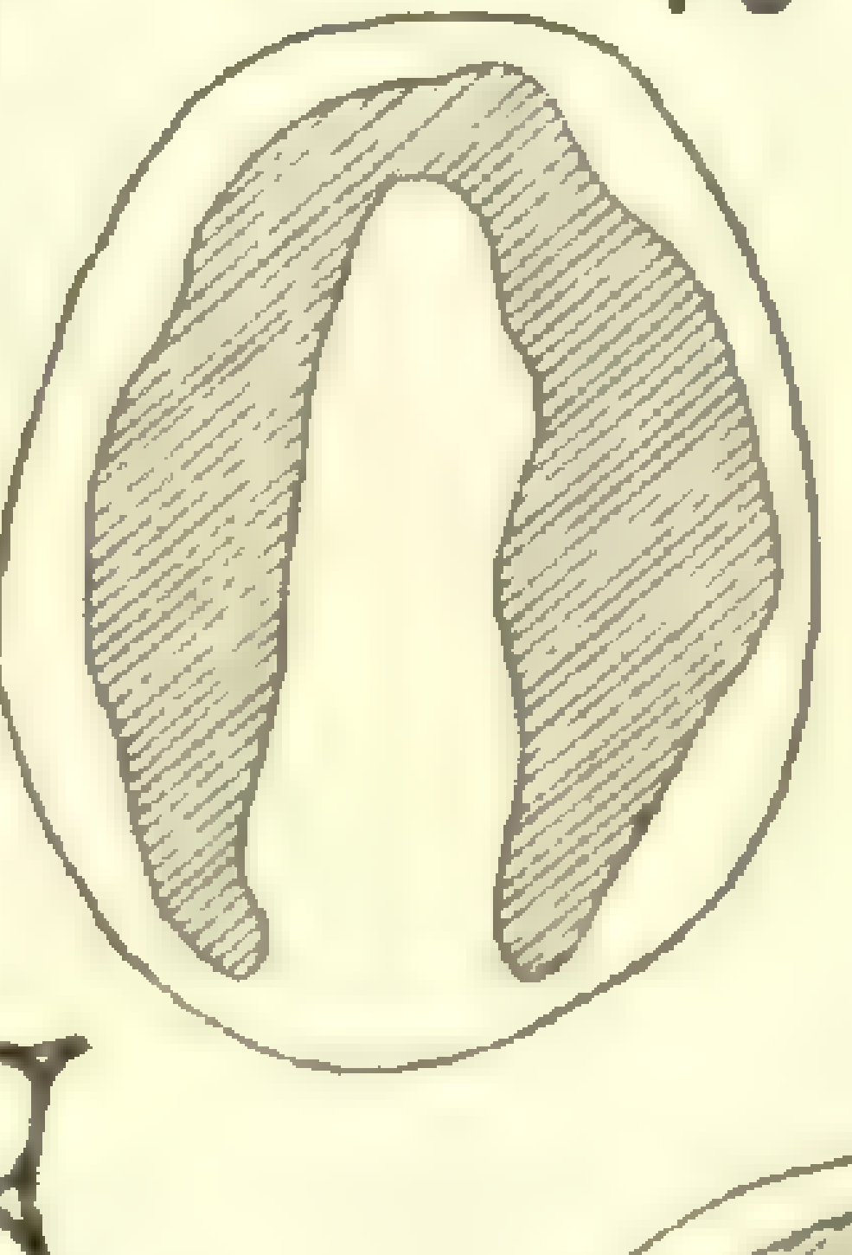

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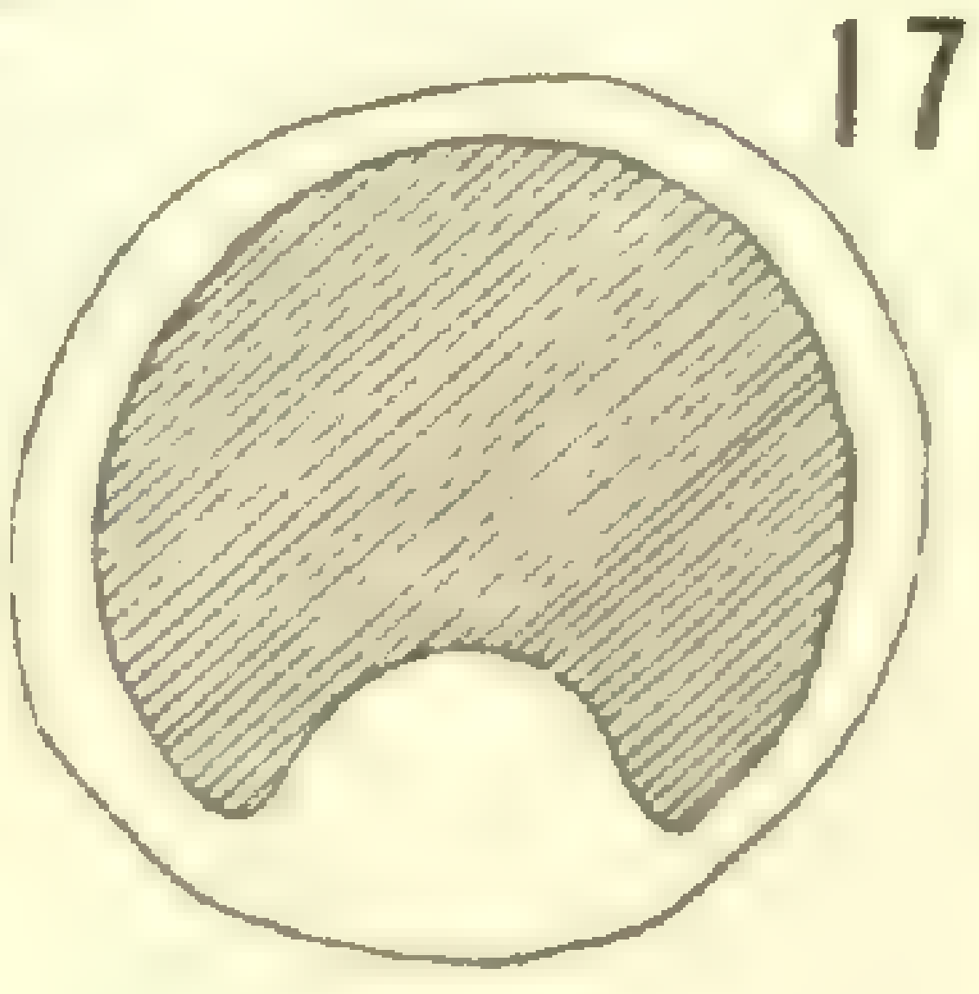

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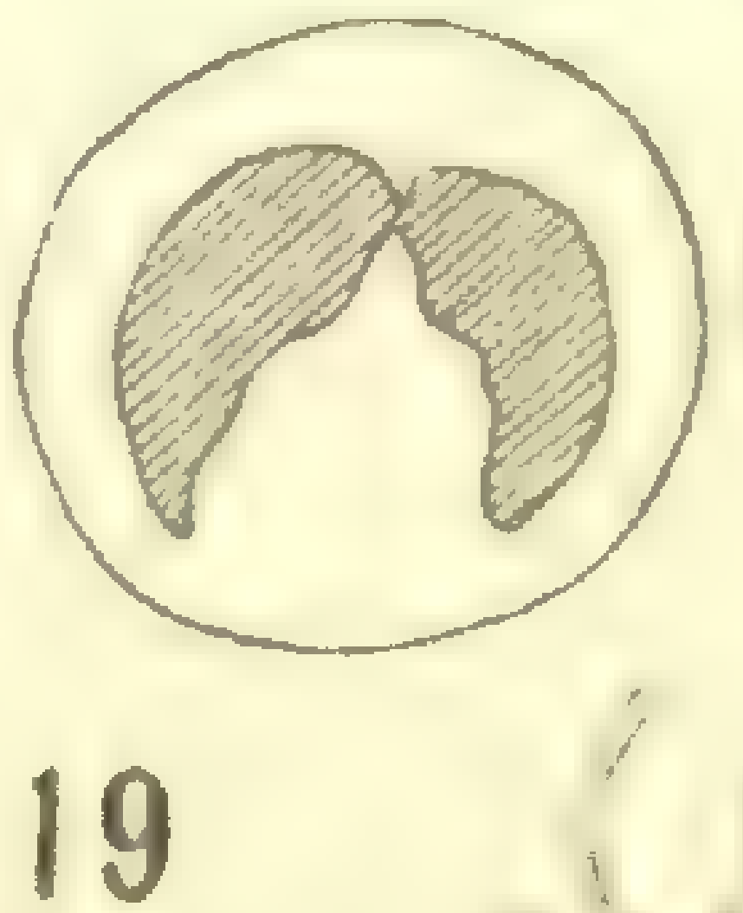

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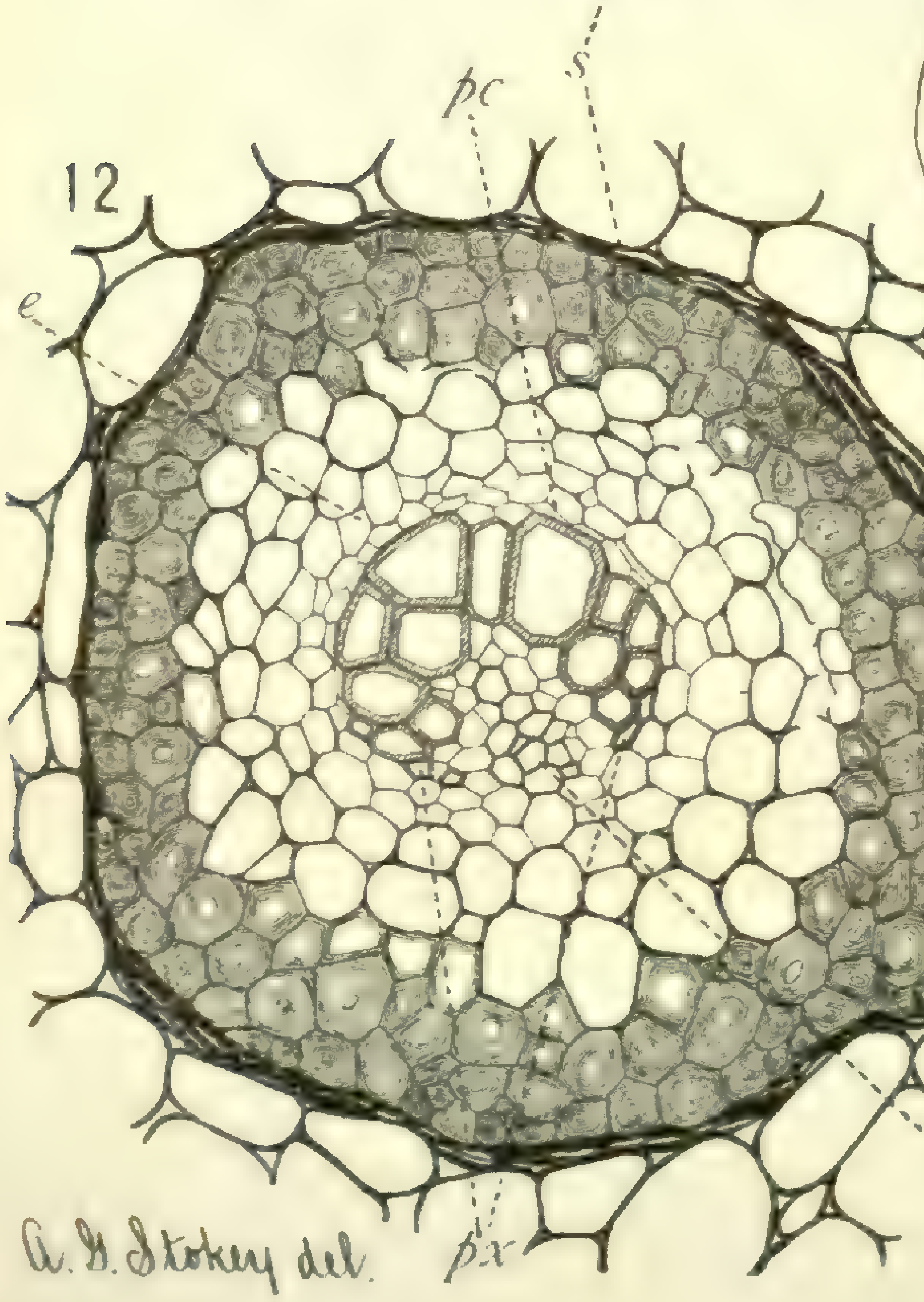

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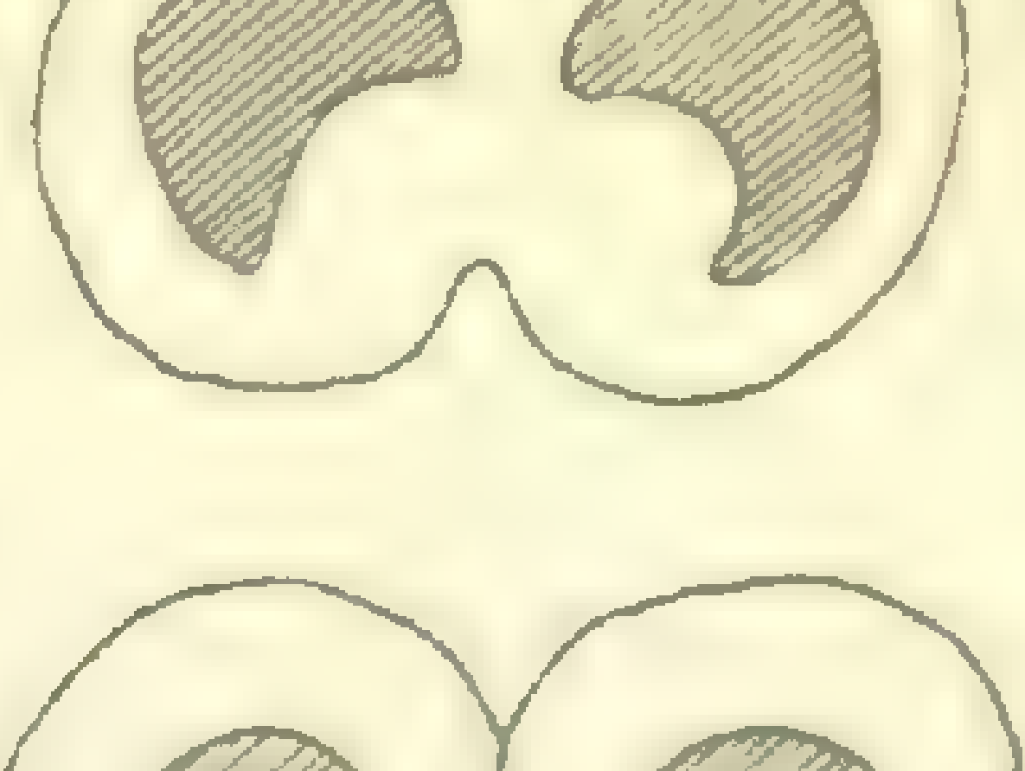

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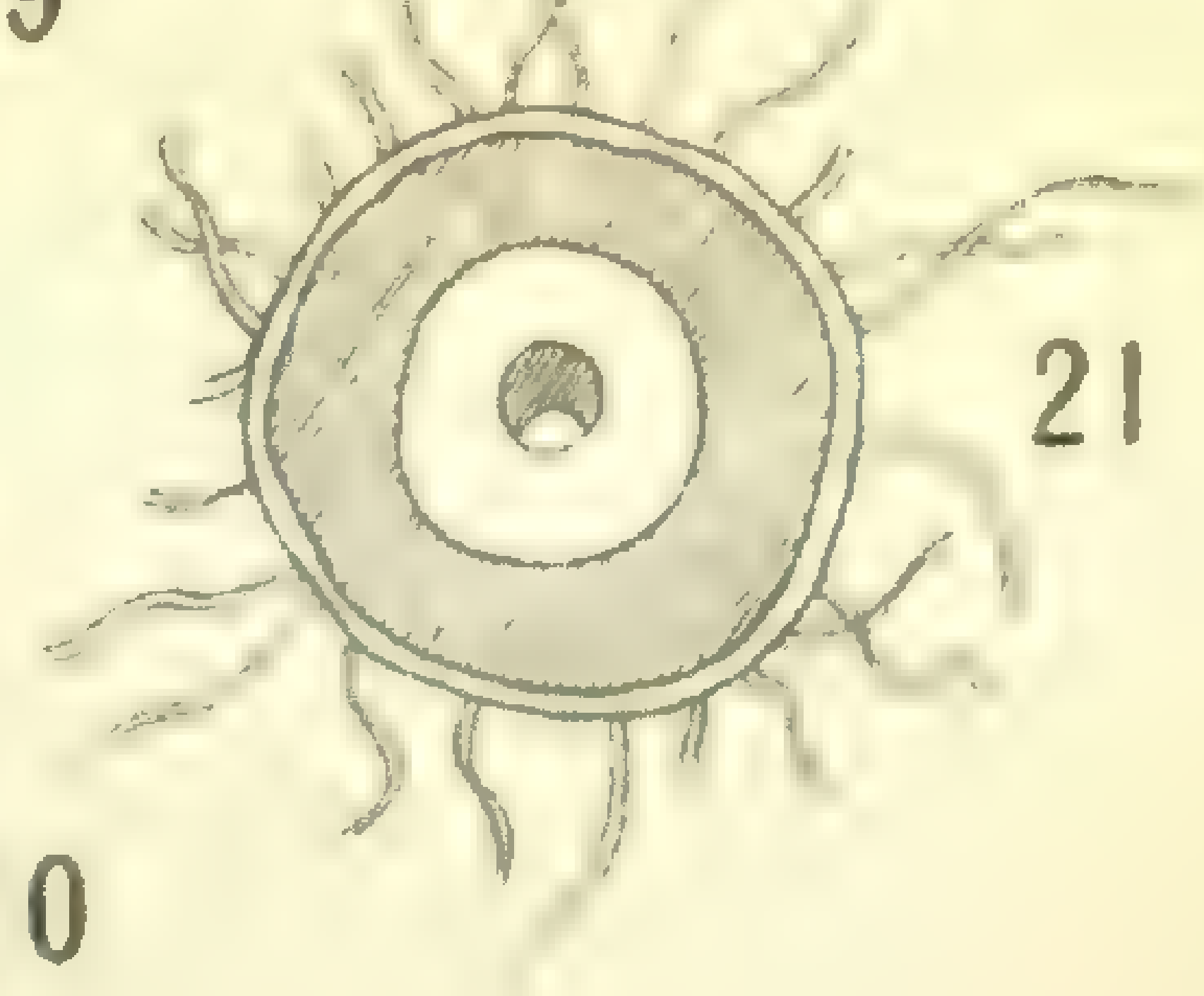

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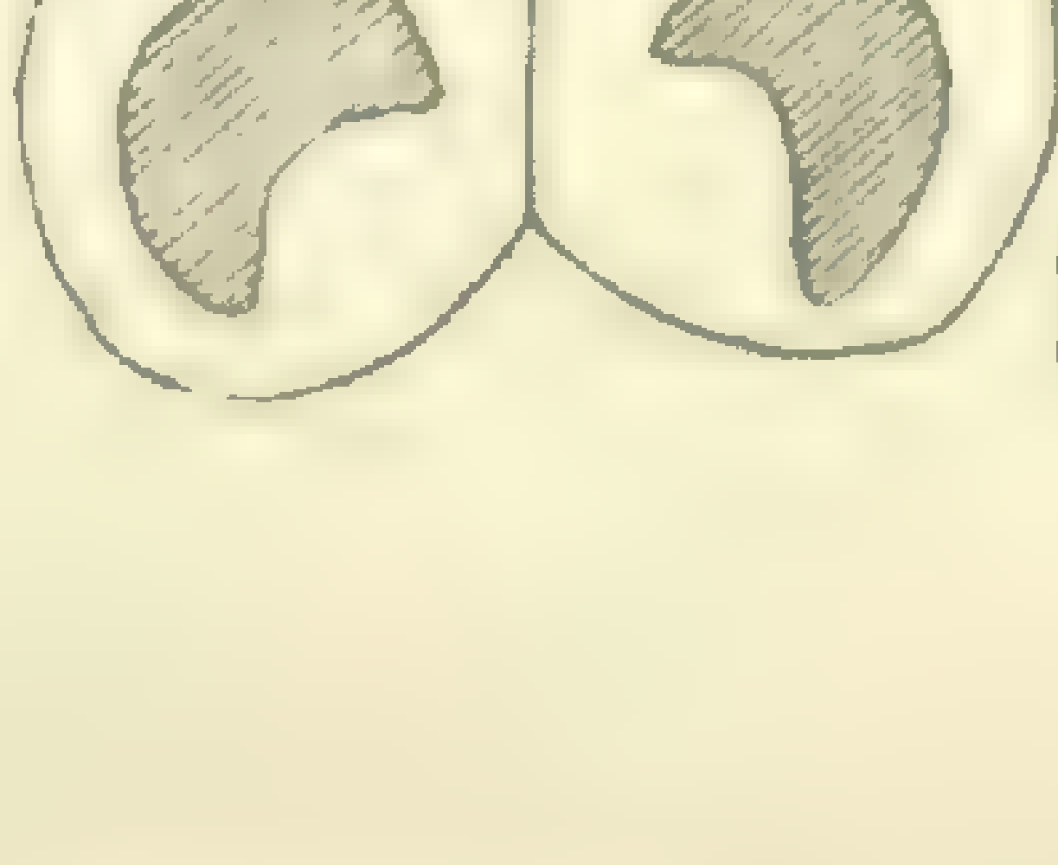

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STOKEY on LYCOPODIUM

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EXPLANATION OF PLATES V AND VI

All the figures were drawn with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are as follows: *x*, xylem; *px*, protoxylem; *ph*, phloem; *e*, endodermis; *pc*, pericycle; *c*, cortex; *sc*, sclerenchyma; *pl*, plerome; *pb*, periblem; *d*, dermatogen; *ca*, calyptrogen; *pr*, primordium.

PLATE V

FIG. 2. Cross-section of stem showing stele surrounded by "inner roots." ×8.

FIG. 3. Cross-section of stem with primordium of root. ×8.

FIG. 4. Primordium of root at its origin from stele of stem. ×160.

FIG. 5. Longitudinal section of root tip. ×160.

FIGS. 6–8. Dermatogen of root showing development of trichomes. ×375.

FIG. 9. Surface view of trichoblast cell which has divided to form two trichomes. ×375.

FIG. 10. Longitudinal section through "inner root" at origin. ×80.

FIG. 11. Diagram of a root-tip of an "inner root," showing dichotomy.

PLATE VI

FIG. 12. Cross-section of "inner root." ×180.

FIG. 13. Cross-section of "inner root" at origin. ×180.

FIG. 14. Cross-section of stele of stem at origin of "inner root" (xylem strands shaded). ×60.

FIG. 15. Cross-section of stele of stem showing root almost separated from stele. ×60.

FIG. 16. Cross-section of stele of root showing shape of xylem just after the root leaves the stele of the stem. ×180.

FIG. 17. Cross-section of stele of root just above the place where the root leaves the stem. ×180.

FIGS. 18–20. Cross-section of stele of root showing division of xylem during forking of the root. ×180.

FIG. 21. Cross-section of external root. ×25.

BRIEFER ARTICLES

THE BLACK-FRUITED CRATAEGUS OF WESTERN NORTH AMERICA

Mr. W. N. SUKSDORF has sent me an interesting series of specimens of black-fruited Crataegus collected by him in the neighborhood of Bingen, Klickitat County, western Washington, and has called my attention to some distinct variations in different individuals of these plants. He groups his plants as follows:

1 (*D*). Plants with normally twenty stamens; fruit usually in few-fruited clusters, generally not more than 8^{mm} in diameter, and ripening sometimes as early as the first of July and sometimes not until the middle of August.

2 (*X*). Plants with rather larger flowers; normally ten stamens; fruit in large drooping clusters often 1 to 1.2^{cm} in diameter and ripening in July. This form seems to be the *C. Douglasii* Lindley of English gardens.

3 (*Y*). Plants with normally ten stamens; fruit in few-fruited often erect clusters, usually 8 to 10^{mm} in diameter, and ripening from July to September. This and the following I cannot distinguish from the *X* group.

4 (*Z*). Plants with ten stamens; fruit as small as that of *D* and ripening sometimes as late as September.

The black-fruited thorn of the northwest was discovered by DAVID DOUGLAS, and in 1830 was named by LINDLEY *C. Douglasii* (*Bot. Reg. pl. 810*). The figure in the *Botanical Register* represents the flowers with ten stamens, and in a grafted plant imported from Europe, which I have cultivated for more than thirty years and which I believe to be one of the same strain as the plant formerly in the garden of the Royal Horticultural Society at Chiswick from which LINDLEY'S figure and description were made, the stamens are normally ten, although sometimes by abortion they are as few as five. The stamens of a tree of *C. Douglasii* sent to the Arnold Arboretum many years ago by MAX LEICHTLIN of Baden Baden are mostly twenty, but are sometimes reduced to twelve or fifteen. The two trees in other characters appear identical, and except in the number of the stamens I have been unable to find any character by which these two forms can be safely distinguished.

On all the specimens of this black-fruited form which I have seen the leaves vary from obovate to ovate; they are cuneate at the base, rather coarsely serrate occasionally nearly to the base, and lobed only toward the apex. At the flowering time they are lustrous, covered above with soft white hairs most abundant on the midribs and veins, and pale and more or less villose in the axils of the veins below, later becoming subcoriaceous, dark green, and very lustrous. The flowers vary from 1.2 to 1.4^{cm} in diameter and are produced on long slender glabrous pedicels, in usually 15- or 16-flowered compound corymbs, with linear caducous bracts and bractlets. The broad calyx-tube is quite glabrous and much longer than the wide, entire, or occasionally minutely dentate lobes, acute and bright red at the apex and sparingly villose on the inner surface. The anthers are small and very pale rose color, and the styles are normally five. The fruit is black, short-oblong, crowned by the persistent calyx, with yellow, succulent, rather sweetish flesh; the nutlets, which in many of Mr. SUKSDORF'S specimens are abortive, wrinkled, and much reduced in size, are normally five, obtuse at the ends, slightly ridged on the back, and irregularly penetrated on the inner faces by shallow longitudinal cavities. The branchlets are red or orange-red and very lustrous, and the spines, which are stout and nearly straight, and generally not more than from 1 to 1.5^{cm} in length, occasionally on vigorous branches become nearly 4^{cm} long. *C. Douglasii* is the common species of the northwestern states, extending north into British Columbia, south into northern California, and eastward at least as far as Wyoming.[1]

Of the plants collected by Mr. SUKSDORF, those with twenty stamens and small fruit, placed by him in his group *D*, vary most from what I consider the type of *C. Douglasii*, and although it does not seem possible to distinguish these specifically, they certainly constitute a well-marked variety, for which I suggest the name:

CRATAEGUS DOUGLASII var. **Suksdorfii,** nov. var.—A shrub sometimes 8^{m} high, with numerous stout, erect, and spreading stems.—Banks of the Columbia River and borders of bottom lands, West Klickitat County, Washington, *W. N. Suksdorf*, 1905–1906 (nos. 4034, 4919, 5026, 5031, 5040).

Another plant in this group should also be mentioned. This is a ten-stamened plant with distinctly chestnut-colored fruits, and may be called:

CRATAEGUS DOUGLASII forma **badia,** nov. forma.—It grows on Union Flat, six miles south of Pullman, Washington, with the black-fruited *C.*

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[1] Of the black-fruited Crataegus which grows at a few stations on the northern peninsula of Michigan and on some of the islands of Lake Superior, and which has been referred to *C. Douglasii*, flowers have not been collected and its true specific position cannot be determined at present.

Douglasii which, although it flowers ten days later, it otherwise resembles except in the color of the fruit. This interesting plant has been collected at different times between 1896 and 1902 by *Mr. C. V. Piper* (nos. 2358, 2454, 3599, 3810, and 3826).[2]

The following synopsis of the species of the DOUGLASAE group may aid in the determination of the species:

Anthers slightly tinged with rose color; calyx-lobes entire or minutely dentate, sparingly villose on the inner surface; fruit short-oblong to subglobose; nutlets 5, obtuse at the ends, slightly ridged on the back, irregularly penetrated on the inner face by shallow longitudinal grooves.

Leaves subcoriaceous, very lustrous, obovate to broadly ovate, coarsely serrate, usually lobed toward the apex, more or less villose while young, generally becoming glabrous; stamens 5–20, normally 10; spines numerous, usually short and stout. . . . . 1. *C. Douglasii.*

Leaves thinner, lanceolate to oblong-obovate, acute at the ends, finely serrate, not lobed, covered above while young with soft white hairs, soon glabrous; stamens 10; spines few, long and slender or wanting . . . 2. *C. rivularis.*[3]

—C. S. SARGENT, *Arnold Arboretum.*

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[2] *C. Gaylussacia* Heller (Bull. South. Cal. Acad. Sci. **2**:68. 1903) is one of the black-fruited group and was collected by HELLER, August 20, 1902, at Sebastopol in Sonoma County, California. Flowers have not been seen, and I suspect that it will turn out to be one of the small-fruited forms of *C. Douglasii.* The leaves are smaller, however, and rather thinner than those of the ordinary forms of that species, and they are still slightly hairy on the upper surface at the end of August when the fruit appears to have been fully ripe.

[3] *C. rivularis* is a more southern species than *C. Douglasii* and is confined to the interior of the continent. It is most abundant on the Wasatch Mountains of Utah and ranges to southwestern Colorado and western Wyoming.

CURRENT LITERATURE

MINOR NOTICES

Mechanics of cell division.—In a study of the mechanics of cell division, GIESENHAGEN[1] presents the following conclusions. The nucleus, even in the resting condition, has a definite polarity, so that it can divide only in a predetermined direction. The median plane in which the cell plate will appear at mitosis is the equatorial plane, and the axis is perpendicular to its center. The axis of the nucleus is definitely determined by the preceding mitosis, its most common position being that of the axis of the mother cell, or a position at right angles to the axis of the mother cell. If the nuclei maintain their positions without any movement, there will be a succession of anticlines and periclines, but many causes may change the position of the nucleus and affect the direction of its axis and consequently the plane of the wall to be formed when the nucleus divides. The numerous variations from the periclinal and anticlinal divisions are discussed and suggestions are made as to their causes.—CHARLES J. CHAMBERLAIN.

American Breeders' Association.—The proceedings of the meeting held at Lincoln, Nebraska, January 17–19, 1906, have just been published as the second volume issued by the Association. Naturally the papers vary widely in subject and in value, and it is impossible to estimate them by reading. It is clear, however, that fundamental biological problems are being considered; and that views and data are being recorded that are extremely suggestive. Among the strictly botanical topics may be noted the following: Tobacco breeding, The corn plant as affected by date of planting, Some correlated characters in wheat and their transmission, Plant adaptation, A method of breeding a strain of alfalfa from a single individual, Correlation of characters in plant breeding, Variation in wheat hybrids, Breeding drought-resistant crops, Fundamental requirements for grain breeding, Value of corn pollen from suckers *vs.* main stalks, A theory of heredity, etc.—J. M. C.

The Dillenian Herbaria.—The herbarium of the University of Oxford contains some collections of great historical interest, among which those of DILLENIUS (1684–1747), the first "Sherardian" professor of botany, are conspicuous. An account of the Dillenian herbaria has just been published, together with a biographical sketch, selections from correspondence, etc., by DRUCE,[2] edited and with an introduction by VINES, the present "Sherardian" professor. The collections of DILLENIUS relate to "subjects so diverse as the investigation of the British Flora, especially that of Wales; the botanical exploration of North America; the botany of the exotics, especially succulents, cultivated in his time; and the classification of cryptogamic plants." The Dillenian herbaria are three: that of the *Synopsis;* that of the *Hortus Elthamensis;* and that of the *Historia Muscorum.*—J. M. C.

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[1] GIESENHAGEN, K., Studien über die Zellteilung im Pflanzenreiche, ein Beitrag zur Entwickelungsmechanik vegetabilischer Gewebe. 8vo. pp. 91. Stuttgart: Fr. Grub. 1905.

[2] DRUCE, G. CLARIDGE, and S. H. VINES, The Dillenian herbaria. pp. cxii + 258. Oxford: The Clarendon Press. 1907. 12 *sh.*

Plant chemistry.—The original papers and addresses on plant chemistry, published by HELEN C. DeS. ABBOTT MICHAEL (*b.* 1857, *d.* 1904), have been collected and reprinted, together with a biographical sketch (110 pp.) and four literary papers, to form a neat volume.[3] Mrs. MICHAEL'S scientific training was obtained under extraordinary difficulties, and her work was made somewhat scattering by reason of the very alertness and eagerness of her mind. Her contributions to a knowledge of the constituents of plants, especially the glucosides, are more valuable than her theories as to the correlation of plant form and classification with the nature and distribution of chemical compounds. The book in its editing shows some unfamiliarity with scientific names and terms. It is a worthy memorial to one whose work was cut short by an untimely death.—C.R.B.

Flora of Guatemala.—JOHN DONNELL SMITH has published as the eighth part of his *Enumeratio* an index[4] of the preceding parts. The species are arranged alphabetically, and 7979 numbers are cited, representing 3736 species, 1189 of which are not contained in HEMSLEY'S *Biologia Centrali-Americana.* Incorrect determinations and faulty nomenclature are also corrected. The author is to be congratulated on the complete way in which he has investigated the flora of this region and organized his results.—J. M. C.

London botanic gardens.—M. PERRÉDÈS has brought together in a single publication[5] a series of papers that appeared in the *American Journal of Pharmacy.* The three gardens described are Kew Gardens, The Royal Botanic Society's Gardens in Regent's Park, and The Chelsea Physic Garden. The numerous admirable illustrations that accompany the text make these gardens very real to the reader.—J. M. C.

Pflanzenfamilien.[6]—Parts 227 and 228 contain the completion of the Lembophyllaceae, and the presentation of Entodontaceae, Fabroniaceae, Pilotrichaceae, Nematoceae, and Hookeriaceae, by V. F. BROTHERUS. The third part of the second supplement continues the literature of 1899–1904 in reference to dicotyledons from Euphorbiaceae to Sapotaceae.—J. M. C.

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[3] MICHAEL, H. A., Studies in plant and organic chemistry. 8vo. pp. 423. Cambridge: The Riverside Press. 1907. $2.50.

[4] SMITH, JOHN DONNELL, Enumeratio plantarum Guatemalensium etc. Pars VIII. pp. 221. Oquawka, Illinois: H. N. Patterson. 1907.

[5] PERRÉDÈS, PIERRE ÉLIE FÉLIX, London Botanic Gardens. pp. 100. *pls. 31.* London: The Wellcome Chemical Research Laboratories. 1907.

[6] ENGLER, A., und PRANTL, K., Die natürlichen Pflanzenfamilien. Lief. 227 und 228 und Ergänzungsheft II, Lief. 3. Leipzig: Wilhelm Engelmann. 1907.

Flora of Winneshiek Co., Iowa.—SHIMEK[7] has published an account of the plants of one of the counties of Iowa, prefacing the annotated list by a discussion of the forest problem, ornamental plants, forage plants, weeds, and medicinal plants.—J. M. C.

Eucalyptus.—The eighth part of MAIDEN'S[8] revision of Eucalyptus contains the description, synonymy, range, and affinities of seven species. This series, begun in 1903, now includes twenty-four species.—J. M. C.

Das Pflanzenreich.[9]—Part 28 contains the group Calceolarieae of Scrophulariaceae. The three genera are Porodittia (1 sp.), Jovellana (6 spp.), and Calceolaria (192 spp., with 9 new).—J. M. C.

NOTES FOR STUDENTS

Apogamy and apospory in ferns.—Professor FARMER and Miss DIGBY have published[10] the results of their studies of apogamy and apospory in ferns. The forms described are *Lastrea pseudo-mas* vars. *polydactyla* Wills, *polydactyla* Dadds, and *cristata apospora* Druery; *Athyrium Filix-foemina* vars. *clarissima* Jones, *clarissima* Bolton, and *uncoglomeratum* Stansfield; and *Scolopendrium vulgare* var. *crispum Drummondae.*

In *Athyrium Filix-foemina clarissima* Jones there is no change in the number of chromosomes in passing from the sporophyte to the gametophyte phase of the life-history; and there is no migration of nuclei from one prothallial cell to another. The embryo arises as a bud upon the gametophyte.

In *Athyrium Filix-foemina clarissima* Bolton there is no reduction of chromosomes, no true fertilization, no migration of prothallial nuclei, and the embryo develops from an unfertilized egg.

In *Athyrium Filix-foemina uncoglomeratum* Stansfield the embryo arises in connection with an archegonium, but details were not discovered. The number of chromosomes (about 100) is maintained throughout the life-history and there is no migration of prothallial nuclei.

In *Scolopendrium vulgare crispum Drummondae* a remarkable condition is described. The number of chromosomes in sporophyte nuclei is about 100, in prothallial nuclei about 70, in archegonial nuclei about 80, and in antheridial nuclei between 70 and 82. There is no cyclic alteration in the number of chromosomes, and no migration or fusion of nuclei of prothallial cells. The embryo arises from the unfertilized egg.

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[7] SHIMEK, B., Flora of Winneshiek County. Iowa Geol. Surv. **16**:147–211. 1906.

[8] MAIDEN, J. H., A critical revision of the genus Eucalyptus. Part VIII. pp. 211–254. *pls. 37–40.* Sydney: Published by State of New South Wales. 1907. *2s. 6d.*

[9] ENGLER, A., Das Pflanzenreich. Heft 28. Scrophulariaceae Antirrhinoideae-Calceolarieae von Fr. Kränzlin. pp. 128. *figs. 21 (142).* Leipzig: Wilhelm Engelmann. 1907. *M*6.40.

[10] FARMER, J. BRETLAND, and L. DIGBY, Studies in apogamy and apospory in ferns. Annals of Botany **21**:161–199. *pls. 16–20.* 1907.

In *Lastrea pseudo-mas polydactyla* Wills, the authors still maintain their claim, made in a preliminary paper, that there is a migration and fusion of prothallial nuclei, thus initiating the sporophytic phase. There is a normal reduction of chromosomes.

In *Lastrea pseudo-mas polydactyla* Dadds there is a reduction of chromosomes and the sporophyte is initiated by a migration and fusion of prothallial nuclei. The embryo, however, comes from a projection which may be regarded as an arrested archegonium.

In *Lastrea pseudo-mas cristata apospora* Druery there is no reduction of chromosomes and no migration of prothallial nuclei. The number of chromosomes shows a remarkable variation, there being 60 in nuclei of prothallial cells, about 78 in nuclei of the embryo, and about 90 in nuclei of antherozoids.

These various forms may be arranged in two categories, one in which spores are produced in connection with the usual reduction of chromosomes; and the other in which there is no spore formation or reduction of chromosomes, the embryo appearing as an outgrowth from the sporophyte. The wide variation in the number of chromosomes is not thought to be due to inaccuracy in counting, but to a real difference. The authors believe that the fluctuation might seem to negative any value being attached to the number of chromosomes.

After a lengthy discussion a general conclusion is drawn which is quite at variance with current notions, namely that there is no necessary correlation between the periodic reduction in the number of chromosomes and alternation of generations. Fertilization and reduction, however, are recognized as holding a definite causal relation to each other, but without assuming any necessary connection between either of them and any other features in the life-history.—CHARLES J. CHAMBERLAIN.

Apogamy in Marsilia.—While investigating apogamy in Alchemilla, STRASBURGER[11] realized the desirability of examining apogamy in other groups. Since Marsilia had been reported to produce embryos without fertilization, he secured material from various botanists, and even obtained sporocarps from specimens in the Kew and Berlin herbaria. Some of the sporocarps, known to have been collected more than thirty years ago, germinated readily.

In some species, notably *M. Drummondii*, the megaspores when isolated from microspores produce prothallia and embryos almost as abundantly as when microspores are present. Sections show that embryos often develop from eggs without fertilization, and that nuclei of these embryos have 32 chromosomes, the $2x$, diploid, or sporophyte number, as was found by comparing mitoses in root tips and other vegetative structures. Megaspores are formed which have $2x$ chromosomes in their nuclei, the reduction of chromosomes having failed to take place. Such megaspores form prothallia whose nuclei have $2x$ chromosomes, and finally an egg is formed with $2x$ chromosomes, and this egg develops an embryo with $2x$ chromosomes; so that the sporophyte number of chromosomes is maintained throughout the life-history. But in the same species there are instances of reduction of chromosomes, so that prothallia and egg have the x or gametophyte number.

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[11] STRASBURGER, E., Apogamy bei Marsilia. Flora **97**:123–191. *pls. 3–8.* 1907.

In forms which produce apogamous embryos, microsporogenesis is likely to be abnormal, the development often stopping before the nucleus of the microspore mother cell divides; but here again normal microspores with the reduced number of chromosomes are sometimes formed. The nuclei of the x and $2x$ prothallia can be distinguished in a general way by their size, the diameter of the nuclei in $2x$ prothallia being about one-third greater than those in x prothallia; also the diameter of the eggs with $2x$ chromosomes is about one-fourth greater than that of eggs with the reduced number.

STRASBURGER uses the term apogamy rather than parthenogenesis because he regards an egg with $2x$ chromosomes as a purely vegetative cell. He would use the term parthenogenesis only in case an egg with x chromosomes should develop an embyro without fertilization. Even if $2x$ chromosomes should appear at the first mitosis in such an egg, he would still regard it as a genuine case of parthenogenesis.

The preparations naturally showed many stages in the development of spore membranes. Shortly before the spore reaches the periphery of the vesicle containing it, the perinium appears. This is a delicate, fine-pored membrane (*Häutchen*) laid down upon the surface of the vesicle by the surrounding tapetal plasmodium. The prismatic layer is then laid down upon the delicate membrane. The exine, mesopore, and endospore are then developed in succession upon the protoplast of the spore. This study supports the view that cell membranes arise only in direct relation with protoplasm.—CHARLES J. CHAMBERLAIN.

Items of taxonomic interest.—S. M. BAIN and S. H. ESSARY (Jour. Mycol. **12**:192, 193. 1906) have described a new anthracnose of alfalfa and red clover (*Colletotrichum trifolii*), which is said to be the most serious plant disease occurring in Tennessee.—J. M. GREENMAN (Field Columbian Mus. Publ. Bot. Ser. **2**:185–190. 1907) has published 10 new species of Citharexylum as preliminary to a synoptical revision of the genus.—E. HASSLER (Bull. Herb. Boiss. II. **7**:161–164. *figs. 5.* 1907) has described a new genus (*Dolichopsis*) of Leguminosae from Paraguay.—L. A. DODE (*idem* 247, 248. *figs. 3*) has described a new species of Juglans (*J. elaeopyren*) from the Santa Catalina Mountains of Arizona; it is distributed in Pringle of 1881 as *J. rupestris* Engelm., and the type is in Herb. Barbey-Boissier.—A. H. MOORE (Proc. Amer. Acad. **42**:521–569. 1907), in a revision of the confused genus Spilanthes, recognizes 63 species; describes as new 2 subsections, 8 species, 4 varieties, and 7 forms; and makes 14 new combinations.—W. H. BLANCHARD (Torreya **7**:55–57. 1907) has described a new Rubus (blackberry) from the vicinity of Philadelphia and Washington.—J. R.

DRUMMOND (Kew Bull. **1907**:90–92) has described a new genus (*Chlamydites*) of Compositae from Tibet.—H. D. HOUSE (Muhlenbergia **3**:37–46. 1907) has described 15 new species of Ipomoea from Mexico and Central America.—REHDER (Rhodora **9**:60–62. 1907) has published a new variety of *Quercus prinoides* from Mass. and N. J.—FINET and GAGNEPAIN (Bull. Soc. Bot. France IV. **6**:55–170. *pls. 9–20.* 1906), in continuation of their *Flore de l'Asie orientale*, have presented the Anonaceae, including 25 genera represented by 249 species, 28 of which are new.—O. E. JENNINGS (Ann. Carnegie Mus. **4**:73–77. *pl. 20.* 1906) has described a new species of Lonicera (*L. altissima*) from Penn.—H. D. HOUSE (Bull. Torr. Bot. Club **34**:143–155. 1907), in his third paper on N. Am. Convolvulaceae, has described a new species of Calycobolus.—K. K. MACKENZIE (*idem* 151–155) has described 4 new western species of Carex.—W. W. ROWLEE (*idem* 157–159) has described 2 new species of Salix from the Canadian Rocky Mountains.—J. M. C.

Riella and Sphaerocarpus.—In the eleventh of his *Archegoniatenstudien* GOEBEL discusses germination and regeneration in these aberrant liverworts,[12] in extension of the investigations recorded in no. IV. Having an abundance of living material, Riella being easily cultivated, he is able to show that the peculiar "wing" of Riella is not an "outgrowth" from an earlier-formed midrib, but that the germ-disk lies in the same plane as the wing and expands directly into the plant (homoblastic development), as soon as the intercalary growing point is organized and becomes active.

Herein he controverts SOLMS-LAUBACH and PORSILD, who seem to consider the development as heteroblastic, holding that the thallus arises, as a different structure, so to speak, from the germ-disk (which SOLMS called protonema and PORSILD the primordial lobe), much as a sphagnum stem arises from its prothallus. GOEBEL (who, however, denies any special interest in such a question), in agreement with PORSILD but contrary to SOLMS, finds no wedge-shaped apical cell in the growing point until a late stage of development. When after injury or under bad conditions adventive shoots are formed, whether on the thallus or germ-disk, there is first the production of simple one-layered regions like the germ-disks, i.e., secondary disks, and from these the new thalli arise directly, as in sporelings.

In Sphaerocarpus the spore produces a germ tube, which at its end becomes a multicellular cylinder with a depressed tip. From one quadrant of the cupped end the vegetative point arises and from two others the wings proceed. The germ cylinder thus produces the thallus homoblastically. In adventive shoots the same phenomena recur. GOEBEL confirms LEITGEB'S statement as to the precocious formation of sex organs, plants only 0.1^{mm} showing their rudiments.[13] The largest sterile thallus found (and this was far beyond the usual) was 1^{mm} long.—C. R. B.

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[12] GOEBEL, K., Archegoniatenstudien. XI. Weitere Untersuchungen über Keimung und Regeneration bei Riella und Sphaerocarpus. Flora **97**:192–214. *figs. 23.* 1907.

[13] Misquoted by CAMPBELL, Mosses and Ferns, 2 ed., 82, as "one millimeter."

Respiration.—In accordance with the theory that in aerobic respiration oxygen acts as a depolarizer,[14] PACKARD finds[15] that when carbohydrates which can be absorbed (e. g., maltose, glucose, fructose) are injected peritoneally into *Fundulus heteroclitus* the resistance to deprivation of oxygen is greatly increased; which the author explains on the assumption that the sugars act as depolarizers. He also concludes that the decrease in resistance to lack of oxygen shown by Fundulus embryos in successive stages of development is due to the using-up of material (probably carbohydrates) stored in the egg.

A paper has been published by HRUBY,[16] which conforms in general to the more modern views as to the nature of respiration; and, though it adds nothing new, it will aid in the propagation of better ideas among European students.

KOSTYTSCHEW reports that *Aspergillus niger* fed with sugar produces little CO_2 under anaerobic conditions in a gaseous medium, but when submerged in a sugar solution it produces CO_2 and alcohol abundantly in the same ratio as in alcoholic fermentation.[17]

PALLADIN and KOSTYTSCHEW concluded that the anaerobic respiration of frozen lupines and stems had nothing to do with alcoholic fermentation.[18] Now they add[19] that alcohol formation (in consequence of anaerobic respiration of seed-plants) only occurs in the presence of carbohydrates; and when they are absent CO_2 is formed without alcohol. The chemics of this sort of anaerobic respiration they leave for further investigation.—C. R. B.

The algal flora of the tropics.—FRITSCH[20] has reached the following conclusions from a study of the subaerial and freshwater algae of the tropics. There is evidence that in the damp tropics there is always a very extensive subaerial algal covering, which probably consists almost entirely of Cyanophyceae, which may thus be regarded as an essentially tropical group. This group may be the descendants of primitive algal forms which existed at earlier periods under conditions analogous to those found in the damp tropics at the present day. Trentepohlia is the only genus of green algae that is really successful in the subaerial flora. In the submerged algal flora of tropical freshwaters the Cyanophyceae also constitute a very important element, though not as preponderant as in the subaerial flora. This freshwater flora is composed of forms in which narrow filaments are much more abundant than broad ones, a fact thought to be related to the small amount of dissolved oxygen in the water. Cladophora and Rhizoclonium are very poorly represented, and Vaucheria and Botrydium are very rare. The Confervales are not very well represented, and probably the Ulotrichales do not attain much development. Spirogyra, on the other hand, is even more abundant in the tropics than in northern latitudes. The desmids show a marked filamentous tendency, which may be due to poor aeration. Oedogonium is very abundant, and the freshwater red algae are not at all uncommon.—J. M. C.

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[14] BARNES, C. R., The theory of respiration. BOT. GAZETTE **39**:96. 1905. MATHEWS, A. P., A theory of the nature of protoplasmic respiration and growth. Biol. Bull. **8**:331. 1905.

[15] PACKARD, W. H., The effect of carbohydrates on resistance to lack of oxygen. Am. Jour. Physiol. **18**:164–180. 1907.

[16] HRUBY, J., Die Atmung der Pflanzen. Beih. Bot. Centralbl. **21**^{1}:156–172. *figs. 3.* 1907.

[17] KOSTYTSCHEW, S., Ueber die Alkoholgärung von *Aspergillus niger*. Ber. Deutsch. Bot. Gesells. **25**:44–50. 1907.

[18] BOT. GAZETTE **42**:397. 1906.

[19] PALLADIN, W., and KOSTYTSCHEW, S., Ueber anaerobe Atmung der Samenpflanzen. Ber. Deutsch. Bot. Gesells. **25**:51–56. 1907.

[20] FRITSCH, F. E., The subaerial and freshwater algal flora of the tropics; a phytogeographical and ecological study. Annals of Botany **21**:235–275. 1907.

Gametophytes and embryo of Libocedrus.—LAWSON[21] has added Libocedrus to the investigated Cupressineae and shows that it agrees in all essential characters with the other genera of the group, as may be seen from the following outline of the results. No prothallial cells are formed in the pollen grain, which at shedding contains the generative and tube nuclei. The pollen tube advances very directly to the archegonial chamber, and upon its arrival the body cell divides to form two large and equal male cells. One to three megaspore mother cells occur and each gives rise to a tetrad. The functioning megaspore becomes filled with endosperm tissue in the usual way, and the megaspore membrane is poorly developed. The archegonia range in number from six to twenty-four, and are grouped in a single complex, invested by a single layer of jacket cells. The ventral canal cell, as in other Cupressineae, is represented only by its nucleus. The contents of the pollen tubes are discharged into the common archegonial chamber, so that both male cells in a tube may function. In fertilization the male slips from its cytoplasmic sheath and unites with the egg nucleus. The two nuclei arising from the division of the fusion nucleus pass to the bottom of the egg and by two successive divisions form eight free nuclei before wall-formation. The cells of the proembryo are arranged in the usual three tiers.—J. M. C.

Evolution of the vascular system of ferns.—TANSLEY[22] has begun the publication of a series of lectures on the evolution of the vascular system of the Filicineae, the first considering the origin of the pteridophytes. The lecturer commits himself to the following positions: that bryophytes and pteridophytes have arisen from the algae independently; that the alternation of generations of the former is "antithetic," of the latter "homologous;" that the prevailing habit of dichotomy among the Filicineae indicates ancestors of the dichotomously branching thallus type, in which the "sporangiferous thallus became specialized for assimilatory functions;" that from such forms the "Filicales, Sphenophyllales, and Equisetales originated, the first group retaining the characters of the primitive type;" and that the Lycopodiales "may perhaps be regarded as an extreme case of leaf reduction in one of these lines."—J. M. C.

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[21] LAWSON, ANSTRUTHER A., The gametophytes and embryo of the Cupressineae with special reference to *Libocedrus decurrens*. Annals of Botany **21**:281–301. *pls. 24–26*. 1907.

[22] TANSLEY, A. G., Lectures on the evolution of the filicinean vascular system. I. New Phytol. **6**:25–35. 1907.

Apogamy in Hieracium.—ROSENBERG[23] finds that in *Hieracium auricula* and *H. venosum* the development of pollen and embryo sacs is normal and fertilization occurs regularly; there are 9 chromosomes in the gametophyte, 18 in the sporophyte, and 27 in the endosperm. Most species of Hieracium, however, are apogamous, and their embryo sacs are formed without any reduction division. Usually they do not arise from megaspores, but from cells of the integument or chalaza; that is, the gametophyte is aposporous and contains the sporophytic number of chromosomes. In *H. excellens* an embryo sac with the reduced number of chromosomes is often formed, but there are usually aposporous sacs in the same head. This shows why *H. excellens*, in spite of its being apogamous, may also produce hybrids.—CHARLES J. CHAMBERLAIN.

Geographic distribution of closely related species.—LEAVITT[24] has published a study of the distribution of species in reference to their evolution. The topics discussed are "the effects of different evolutionary agencies upon specific distribution," "the necessity of isolation and Mendelian inheritance," "specific distribution in the animal kingdom," "the distribution of plants," and "evidence from North American Orchidaceae." The problems are stated and solutions are not attempted, but the impression of the author is that a study of the specific distribution of plants is not likely to be unfavorable to mutation as one method of evolution. He thinks that "the adherents of mutation will be able to bring forward enough cases of social distribution to render phytogeographic weapons useless in the attack upon this theory."—J. M. C.

Cytology of apospory.—*Nephrodium pseudo-mas* Rich. var. *cristata apospora* Druery, according to Miss DIGBY,[25] shows almost all grades of apospory and apogamy except parthenogenesis. Several fronds pegged down quickly produced prothallia at the tips of the leaves, and these prothallia within three weeks bear apogamous embryos. Antheridia are not uncommon, but no archegonia could be found. The number of chromosomes in cells of the leaf, aposporous prothallia, and in the apogamous embryos is about 50, there being no reduction of chromosomes. In *N. pseudo-mas* Rich. var. *polydactyla* Wills, migrating nuclei, some of which have been seen to fuse, are a characteristic feature; while in the var. *cristata apospora* Druery there seems to be no migration or fusion of nuclei. —CHARLES J. CHAMBERLAIN.

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[23] ROSENBERG, O., Cytological studies on the apogamy in Hieracium. Bot. Tidsskrift **28**:143–170. *pls. 1–2.* 1907.

[24] LEAVITT, ROBERT GREENLEAF, The geographic distribution of closely related species. Amer. Nat. **41**:207–240. 1907.

[25] DIGBY, L., On the cytology of apogamy and apospory. II. Preliminary note on apospory. Proc. Roy. Soc. London **76**:463–467. 1905.

Myxomycete studies.—Degenerating nuclei have been observed in young sporangia of various Myxomycetes. JAHN[26] finds that at an early stage in the development of the sporangium nuclei fuse in pairs, and that the degenerating nuclei are those which have failed to fuse. Preceding sporogenesis JAHN claims to have found synapsis and a reduction of chromosomes. In Ceratiomyxa the mature spore has four nuclei. When the spore germinates there is another mitosis, and eight uninucleate swarmspores are produced from the amoeba. Swarmspores, amoebae, and plasmodia seem to have the reduced number of chromosomes, the $2x$ generation being confined to a comparatively short period in the development of the sporangium.—CHARLES J. CHAMBERLAIN.

A bacterial plant-tumor.—SMITH and TOWNSEND[27] have demonstrated that a gall occurring on the cultivated "marguerite" (*Chrysanthemum frutescens*) is caused by a bacterium, for which they propose the name *Bacterium tumefaciens*. The organism was isolated, and in some of the experiments 100 per cent. of the inoculations gave positive results, while the check plants remained free from tumors. As the authors say, "the number of vegetable galls known positively to be due to bacteria is not very great. The discovery of a new one of undoubted bacterial origin, therefore, is of considerable interest to plant pathologists, and may be of some interest to animal pathologists, especially to those interested in determining the origin of cancerous growths."—J. M. C.

Rate of growth in Jamaican forests.—SHREVE[28] has studied the rate of leaf growth in the rain-forest of the Jamaican mountains, and reaches the following conclusions: (1) that the rate of leaf growth is very slow as compared with that in tropical trees in which it has already been measured; (2) that the renewing foliage of deciduous trees does not grow more rapidly than that of evergreen broad-leaved trees; and (3) that the prevalence of conditions unfavorable to photosynthesis and transpiration would seem to offer at least a partial explanation of the slow rates of growth.—J. M. C.

Potato scab.—MORSE[29] has recently published a summary of our present knowledge of the scab of Irish potatoes and of the methods in vogue for its prevention. In addition to the well-known treatment of the uncut tubers with a solution of formaldehyde or with a solution of corrosive sublimate, an account is given of the newer treatment with formaldehyde gas generated by the heat arising from the chemical action due to pouring the formaldehyde over some potassium permanganate. This new method gives very good results and is particularly useful when large quantities of tubers are to be treated.—E. Mead Wilcox.

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[26] JAHN, E., Myxomycetenstudien. 6. Kernverschmelzungen und Reduktionsteilungen. Ber. Deutsch. Bot. Gesells. **25**:23–26. 1907.

[27] SMITH, ERWIN F., and TOWNSEND, C. O., A plant-tumor of bacterial origin. Science N. S. **25**:671–673. 1907.

[28] SHREVE, FORREST, Studies on rate of growth in the mountain forests of Jamaica. Johns Hopkins Univ. Circ. **1907**:no. 3. 31–37.

[29] MORSE, W. J., The prevention of potato scab. Bull. Maine Exp. Sta. **141**:81–92. 1907.

Mitotic figures.—The nature of the forces which determine the achromatic figure is discussed by Hartog,[30] and speculations as to processes occurring in the living cell are illustrated by ingenious experiments. Finely pulverized magnetite under the influence of magnets was made to take the form of the familiar mitotic figures. Photographs of these magnetic figures showing centrosomes, centrospheres, polar radiations, mantle fibers, and central spindles are given. Tripolar and quadripolar spindles were easily produced.—Charles J. Chamberlain.

The xerophytic character of gymnosperms.—Miss Stopes[31] has brought together the data in reference to xerophily among the gymnosperms, and concludes "that the xerophytic characters of the Coniferales in many cases are not adaptations to xerophytic conditions in their own times, nor are they 'inherited' from the remote past as vestigial characters, but are the result of physiological limitations of the type of wood in this ancient and incompletely evolved group. In other words, their 'xerophytism' is not ecological, but phylogenetic."—J. M. C.

Embryogeny of Gnaphalium.—The occurrence of parthogenesis in Antennaria suggested to Schiller[32] an examination of the nearly related genus Gnaphalium. A study of *G. supinum*, *G. silvaticum*, and *G. uliginosum* showed the normal formation of four megaspores in the nucellus, a normal embryo sac with the rather extensive antipodal development characteristic of many Compositae, and the regular occurrence of double fertilization. When pollination is prevented no embryos are formed.—Charles J. Chamberlain.

Course of pollen tube in Sibbaldia.—According to Albanese,[33] the growth of the integument in *S. procumbens* continues until the micropyle is entirely closed. The pollen tube grows through the tissues of the integument and nucellus and thus reaches the embryo sac. This course of the pollen tube and also the described cases of chalazogamy are regarded not as primitive conditions but as variations from the porogamic type. Sibbaldia often shows several embryo sacs in a single nucellus.—Charles J. Chamberlain.

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[30] Hartog, Marcus, The dual force of the dividing cell. Part I. The achromatic spindle figure illustrated by magnetic chains of force. Proc. Roy. Soc. London **76**: 548–675. *pls. 9–11.* 1905.

[31] Stopes, M. C., The "xerophytic" character of the gymnosperms; is it an "ecological" adaptation? New Phytol. **6**:46–50. 1907.

[32] Schiller, Josef, Untersuchungen über die Embryogenie in der Gattung Gnaphalium. Oesterr. Bot. Zeits. **57**:137–142. *pl. 5.* 1907.

[33] Albanese, Nicolò, Ein neuer Fall von Endotropismus des Pollenschlauches und abnormer Embryosacksentwickelung bei *Sibbaldia procumbens* L. Sitzber. Kais. Akad. Wiss. Wien **113**:1–24. *pls. 1–2.* 1904.

Elementary species and hybrids of Capsella.—SHULL[34] has published an extract from his paper at the recent New York meeting of the American Association. The raising of over 20,000 "pedigreed" specimens demonstrated the presence of at least four elementary species that breed true when self-pollinated or crossed within the limits of the same elementary form. The bearing of these experimental results upon questions of plant-breeding under discussion is compactly outlined.—J. M. C.

Sporogonium of Notothylas.—LANG[35] has made a study of the sporogonium of a Notothylas, presumably *N. Breutelii*, growing in the Singapore Botanic Gardens. The embryogeny is in no way different from that of the other Anthocerotales except that more or less of the endothecium is sporogenous. LANG thinks Notothylas is a rather artificial genus which includes a number of forms derived by reduction in size of the sporogonia from one or more Anthoceros-like forms.—W. J. G. LAND.

Sporangium of Equisetum.—HAWKINS[36] has described a situation in the development of the sporangium of *Equisetum hiemale* which is hard to understand. The superficial sporangium initial divides periclinally, as usual, but the inner cell is said to be sterile, and the outer to give rise to the sporogenous tissue, which is certainly not the eusporangiate habit. With this interpretation, the sporogenous tissue is superficially exposed and forms the so-called wall-layers.—J. M. C.

Ovules of Juniperus.—KUBART[37] regards the ovulate structures in Juniperus as a single flower and not as an inflorescence, the ovules being simply transformed leaves, and the ovuliferous scale an aril. The ovulate and staminate flowers show a perfectly analogous structure. The paper contains a short discussion of the phylogeny of gymnosperms.—CHARLES J. CHAMBERLAIN.

Formative substances.—CHILD'S thorough criticism of the hypotheses of "formative substances" as applied to the phenomena of development, regeneration, polarity, etc., in animals deserves attention by botanists, since like general assumptions, which involve special assumptions in an endless chain, have some currency in plant physiology.[38]—C. R. B.

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[34] SHULL, GEORGE H., Elementary species and hybrids of Bursa. Science N. S. **25**:590–591. 1907.

[35] LANG, W. H., On the sporogonium of Notothylas. Annals of Botany **21**:201–210. *pl. 21*. 1907.

[36] HAWKINS, LON A., The development of the sporangium of *Equisetum hyemale*. Ohio Nat. **7**:122–128. *pls. 9–10*. 1907.

[37] KUBART, BRUNO, Die weibliche Blüthe von *Juniperus communis* L. Sitzber. Kais. Akad. Wiss. Wien **114**:1–29. *pls. 1–2*. 1905.

[38] CHILD, C. M., Some considerations regarding so-called formative substances. Biol. Bull. **11**:165–181. 1906.

NEWS

Dr. G. R. Wieland, Yale University, is spending five months in Europe in a study of the collections of cycads.

Francis Darwin has been nominated by the council president of the British Association for its Dublin meeting next year.

Sir Joseph Hooker was awarded the Linnean gold medal of the Royal Swedish Academy at the Linnean bicentenary.

Dr. J. B. Overton, hitherto instructor, has been promoted to be assistant professor of botany in the University of Wisconsin.

F. M. Andrews, associate professor of botany in Indiana University, has leave of absence for a year of study in Germany.

Rob. E. Fries has published an extended account of the life and work of Linnaeus in Engler's *Botanische Jahrbücher* (41:1–54. 1907).

Professor William Trelease received the degree of doctor of laws at the fiftieth anniversary of Washington University, St. Louis.

Dr. Mintin A. Chrysler, instructor in botany in Harvard University has been appointed professor of botany in the University of Maine.

The gold medal of the Linnean Society, London, has been awarded to Dr. Melchior Treub, Director of the Botanical Garden at Buitenzorg.

Dr. Maxwell T. Masters, editor of *The Gardeners' Chronicle*, and especially interested in the classification of conifers, died May 30, at the age of 74 years.

Dr. H. Hasselbring, University of Chicago, has been appointed assistant botanist at the Government Agricultural Experiment Station, Las Végas, Cuba.

Dr. J. E. Kirkwood has been promoted to a professorship of botany in Syracuse University, and the subject is now recognized as a distinct department.

Dr. E. W. Olive, instructor in botany in the University of Wisconsin, has been appointed professor of botany in the Agricultural College of South Dakota.

Dr. Henry C. Cowles, University of Chicago, left on June 20 with a party of twenty-two students, to spend six weeks in Oregon and six weeks in Alaska in ecological study.

F. E. Lloyd has been appointed special investigator in the Agricultural Experiment Station, Tucson, Arizona, to study certain problems connected with the development of the date.

Dr. E. N. Transeau, now at the Carnegie Station for Experimental Evolution at Cold Spring Harbor, has been appointed professor of botany in the State Normal School at Charleston, Ill.

PROFESSOR CHARLES E. BESSEY, University of Nebraska, on May 14 delivered an address on "The Place of Linné in Science" before the Botanical Club of the University of Chicago.

THE UNIVERSITY OF UPSALA, in connection with the commemoration of the bicentenary of Linnaeus, conferred honorary degrees upon W. G. FARLOW, WILLIAM CARRUTHERS, and FRANCIS DARWIN.

ERRATUM.—Three figures were unfortunately misplaced in Mr. H. D. HOUSE'S paper on "New or Noteworthy North American Convolvulaceae," in the June number. Corrections should be made as follows: For *fig. 2*, p. 411, read *fig. 4;* for *fig. 3*, p. 412, read *fig. 2;* and for *fig. 4*, p. 412, read *fig. 3*. The numbers under the three species will then refer to the proper figures.

A PLOT OF GROUND, about four acres in extent, has been set apart by The University of Chicago as a Botanic Garden. It adjoins Washington Park and fronts the Midway Plaisance, and is therefore very near to the botanical laboratory. It is to be strictly a laboratory garden, and will very much extend the facilities for experimental work. This area will be doubled as the plans develop.

THE HERBARIUM of the University of Chicago has been deposited in the Field Museum of Natural History. It contains the collection brought together by Professor COULTER during the period of his activity in taxonomy. This arrangement enables the university to offer facilities for research work in the classification of the higher plants, and incorporates with the collections of the Field Museum sets and types that will soon be made accessible for study in that admirably managed establishment.

IN THE *Bulletin of the Torrey Botanical Club* (34:167–178. 1907) an "American Code of Botanical Nomenclature" is published. It was prepared by the Nomenclature Commission of the Botanical Club of the American Association, after a study of the rules and recommendations adopted by the Vienna Congress of 1905. Exception is taken especially to the failure to recognize the principle of types, to the arbitrary selection of several hundred generic names to be exempt from all rules of nomenclature, to the treatment of homonyms, and to the requirement that after January 1, 1908, all descriptions of new species or genera must be accompanied by a Latin diagnosis. This "American Code" is in effect an announcement that the botanists signing it will not be bound by the rulings of the Vienna Congress; but how far this attitude represents American botanists remains to be seen. The BOTANICAL GAZETTE, while not in full accord with all the rulings of the Vienna Congress, is decidedly in favor of any international agreement that will bring some measure of uniformity. While the "American Code" contends for certain principles, some of which doubtless should be contended for in an international congress, the most important principle to be established is international agreement

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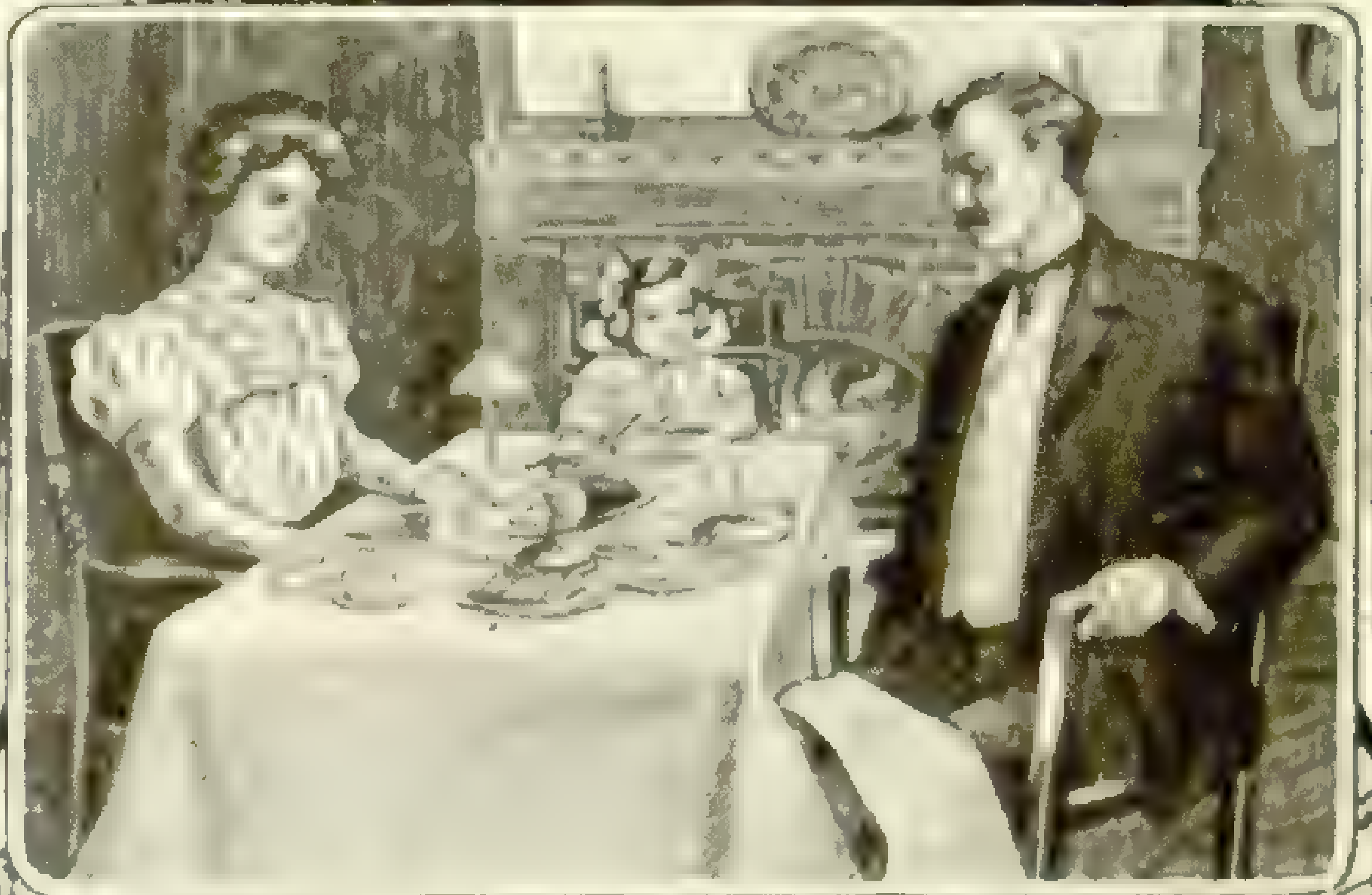

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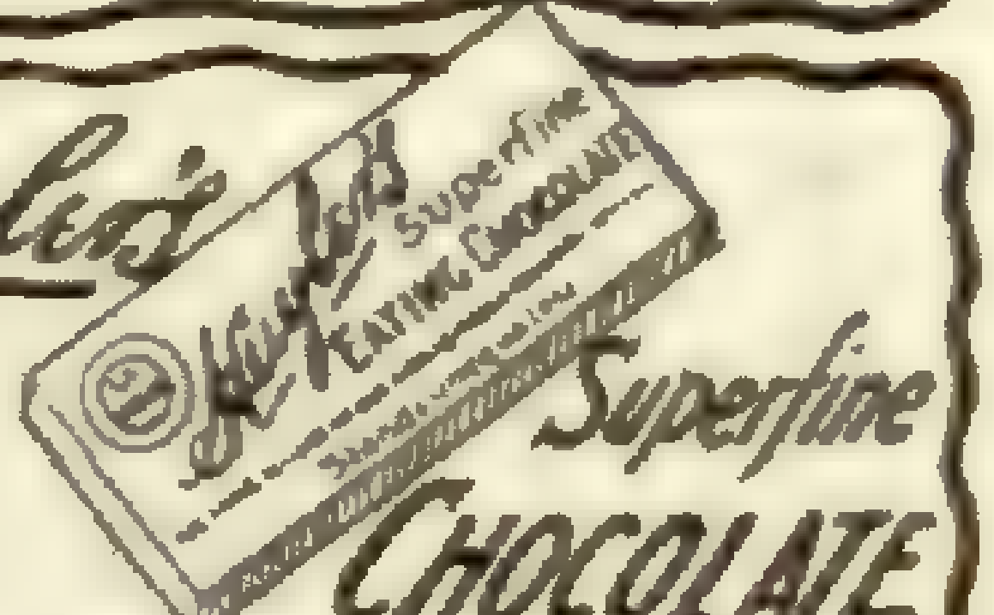

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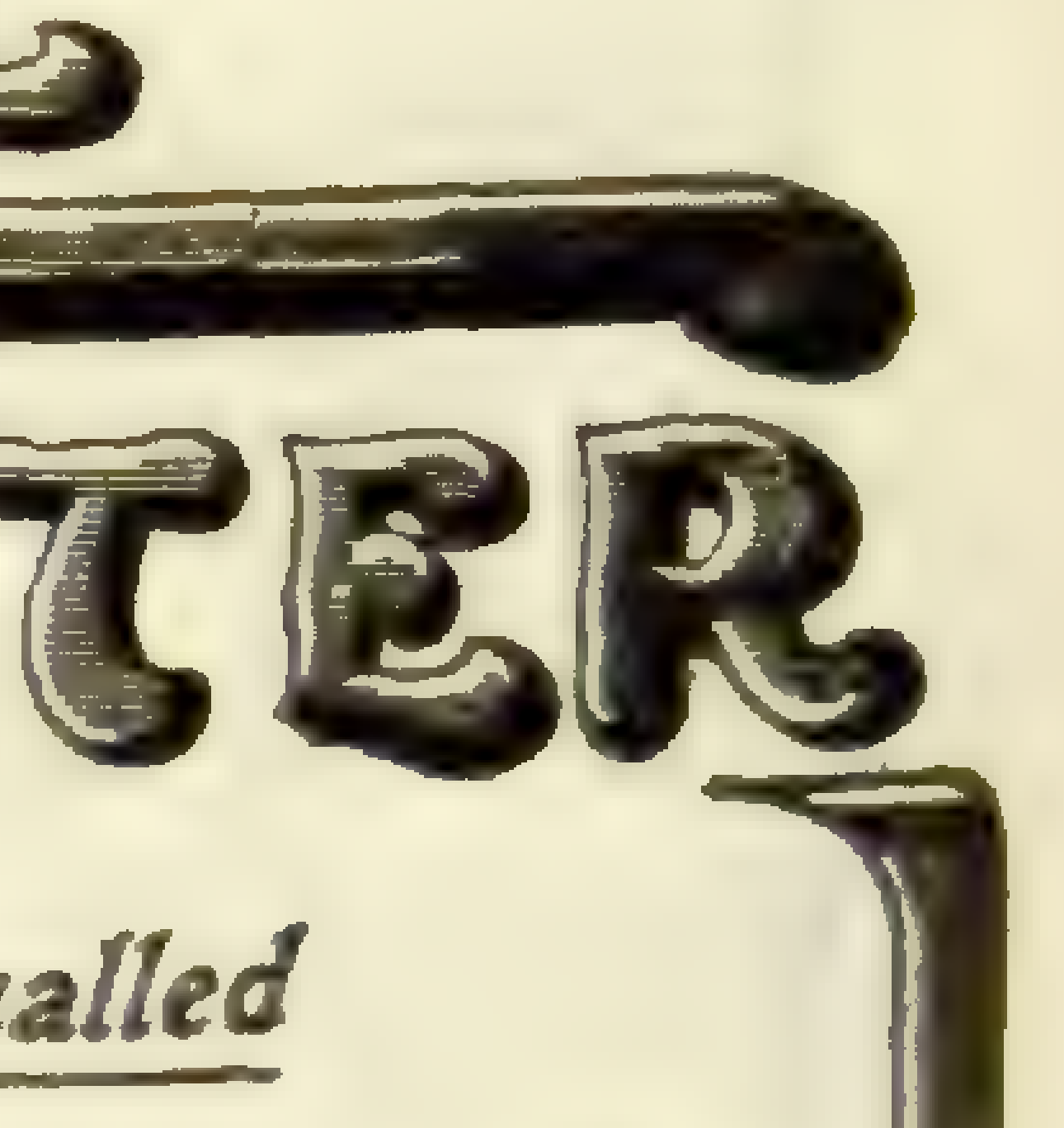

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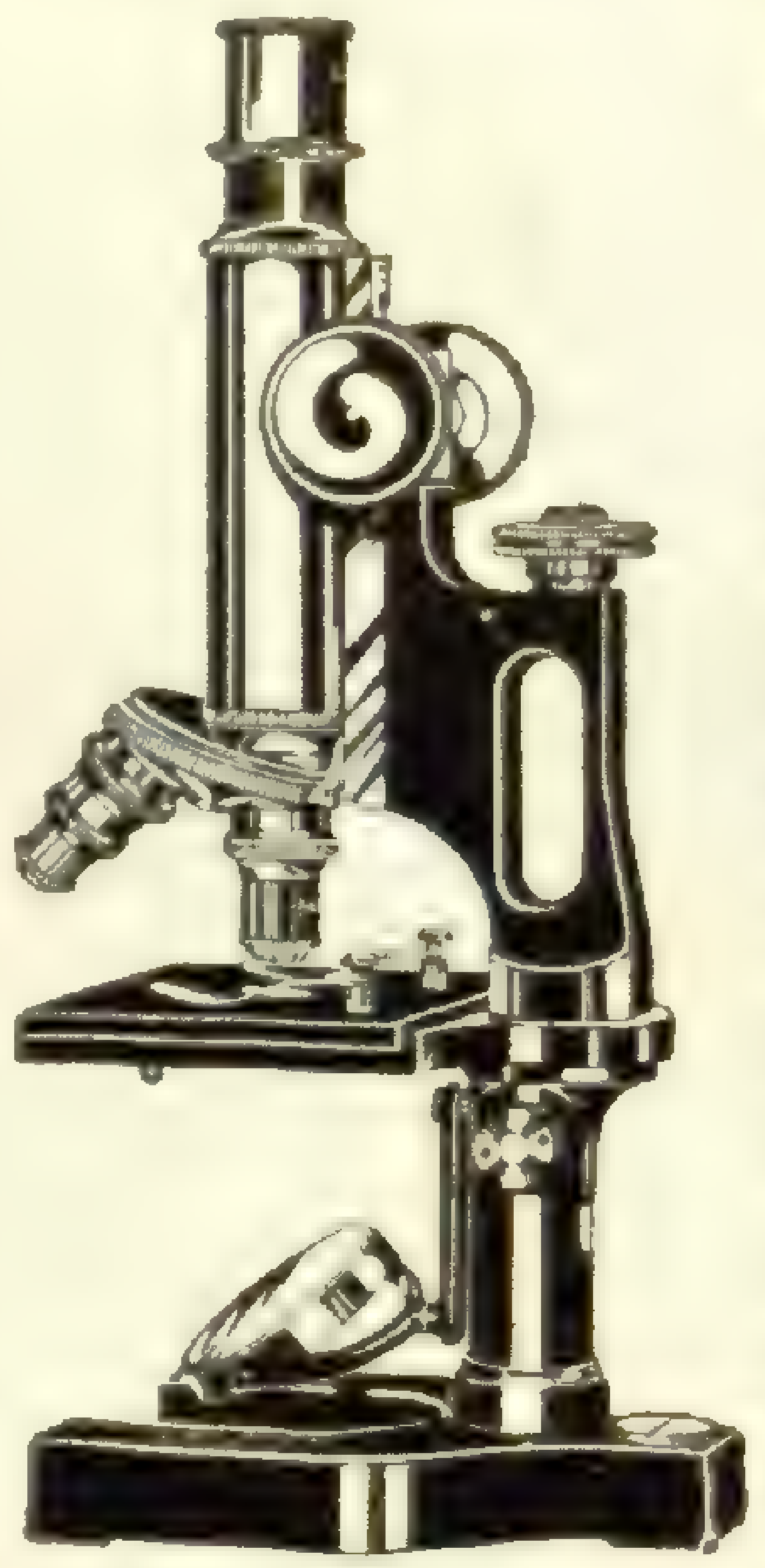

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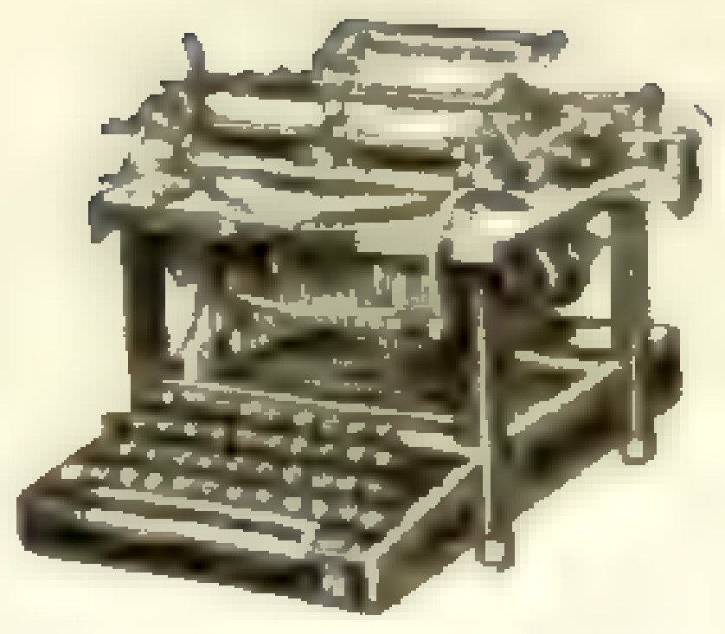

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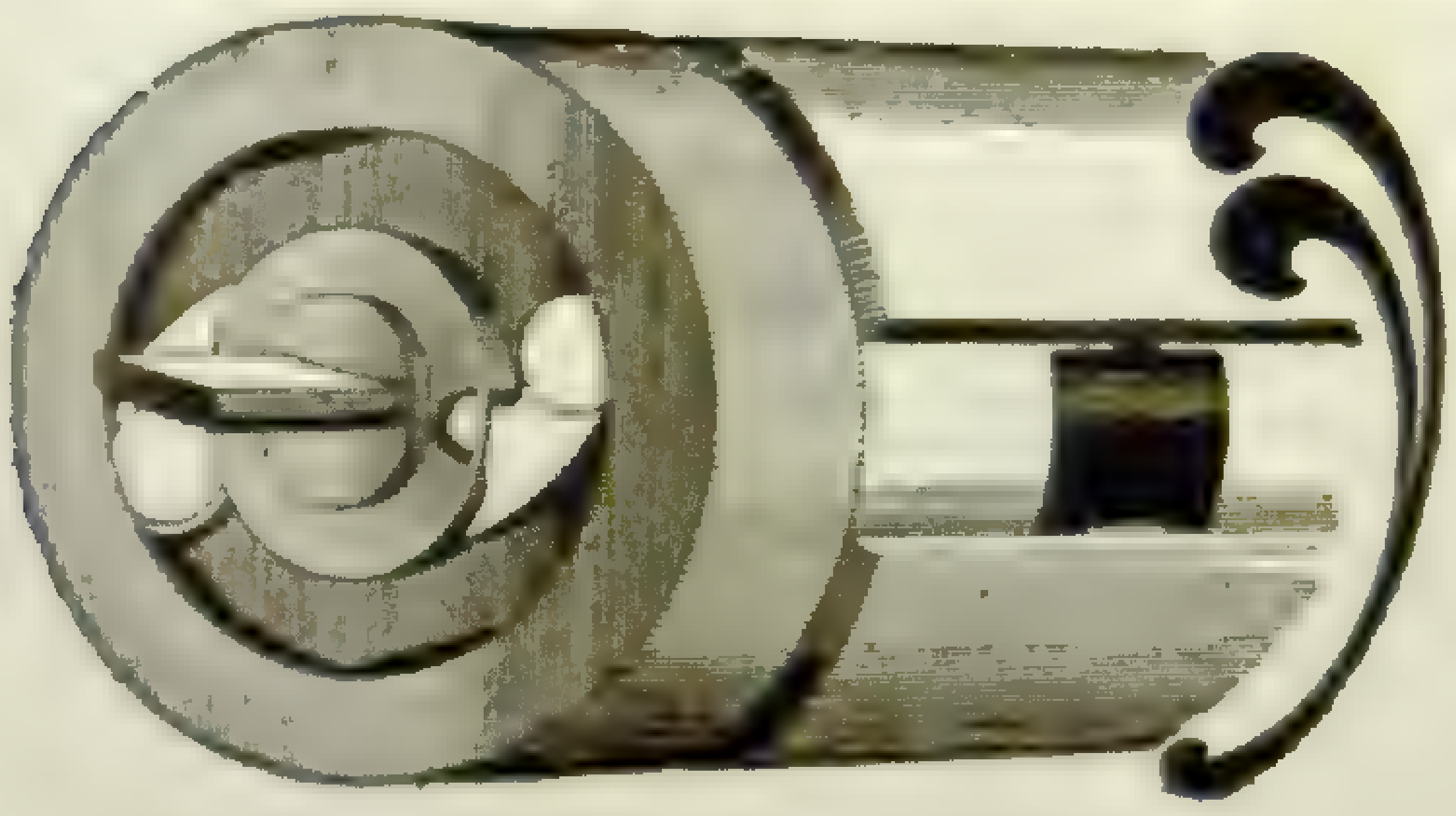

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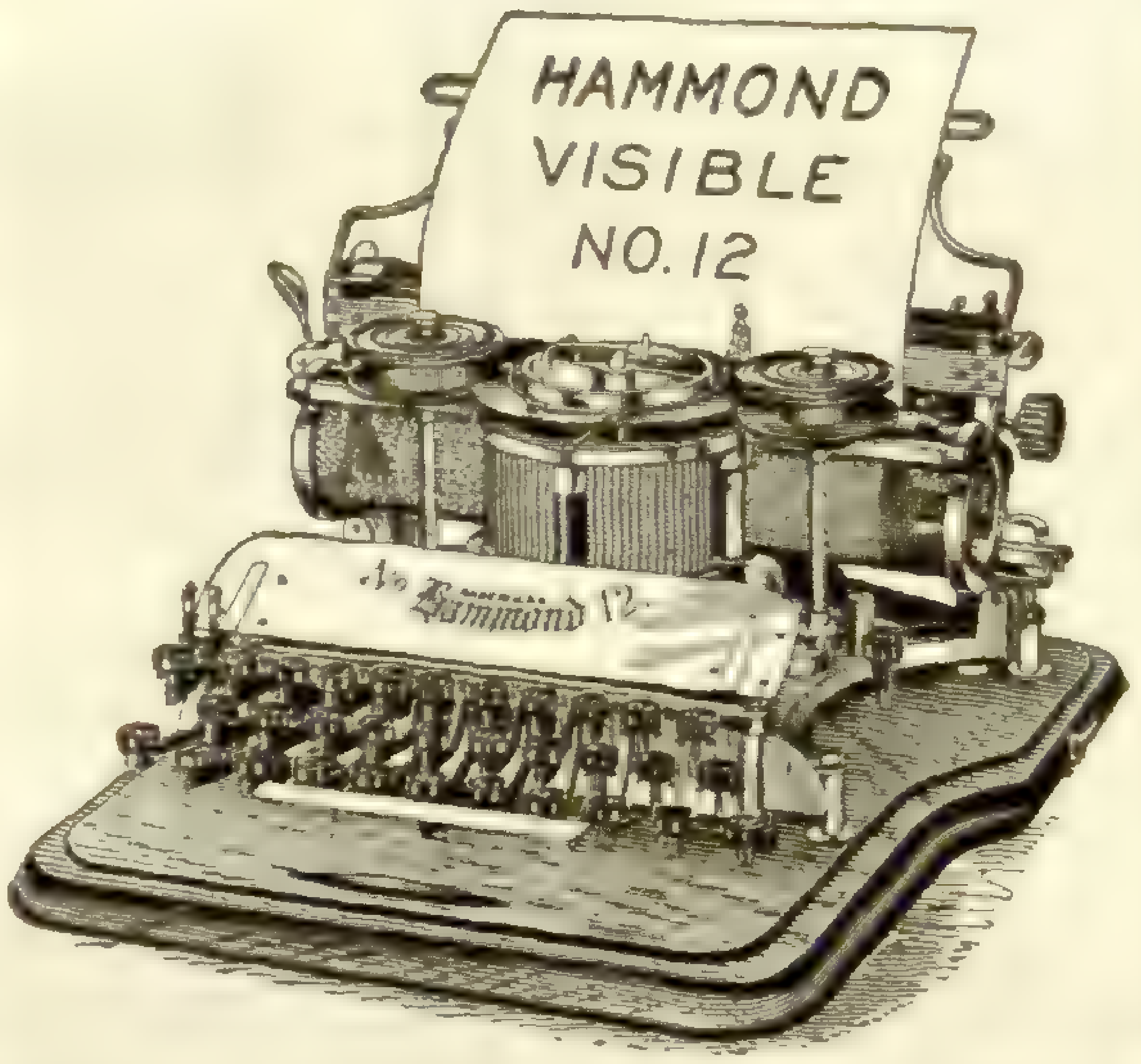
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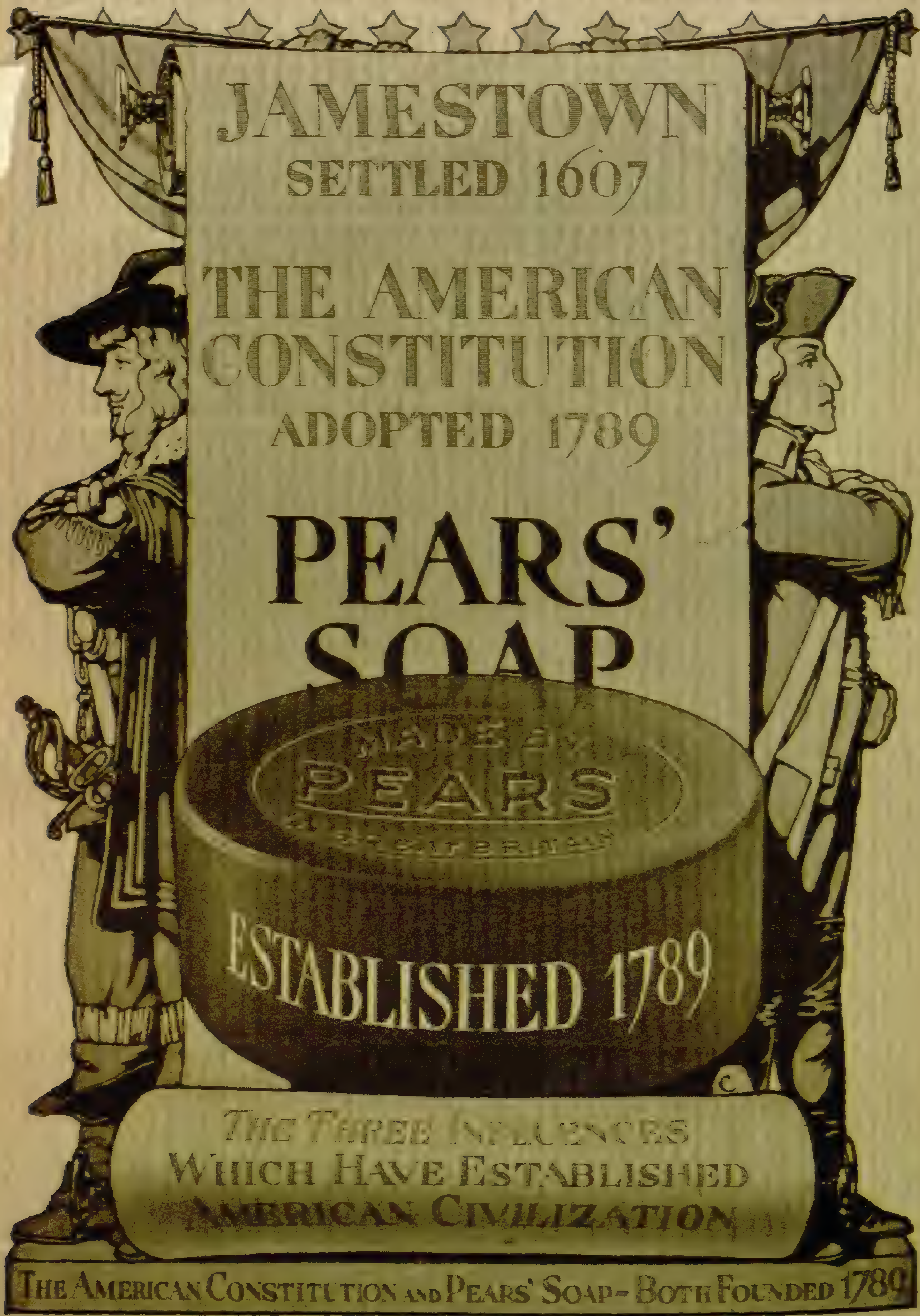
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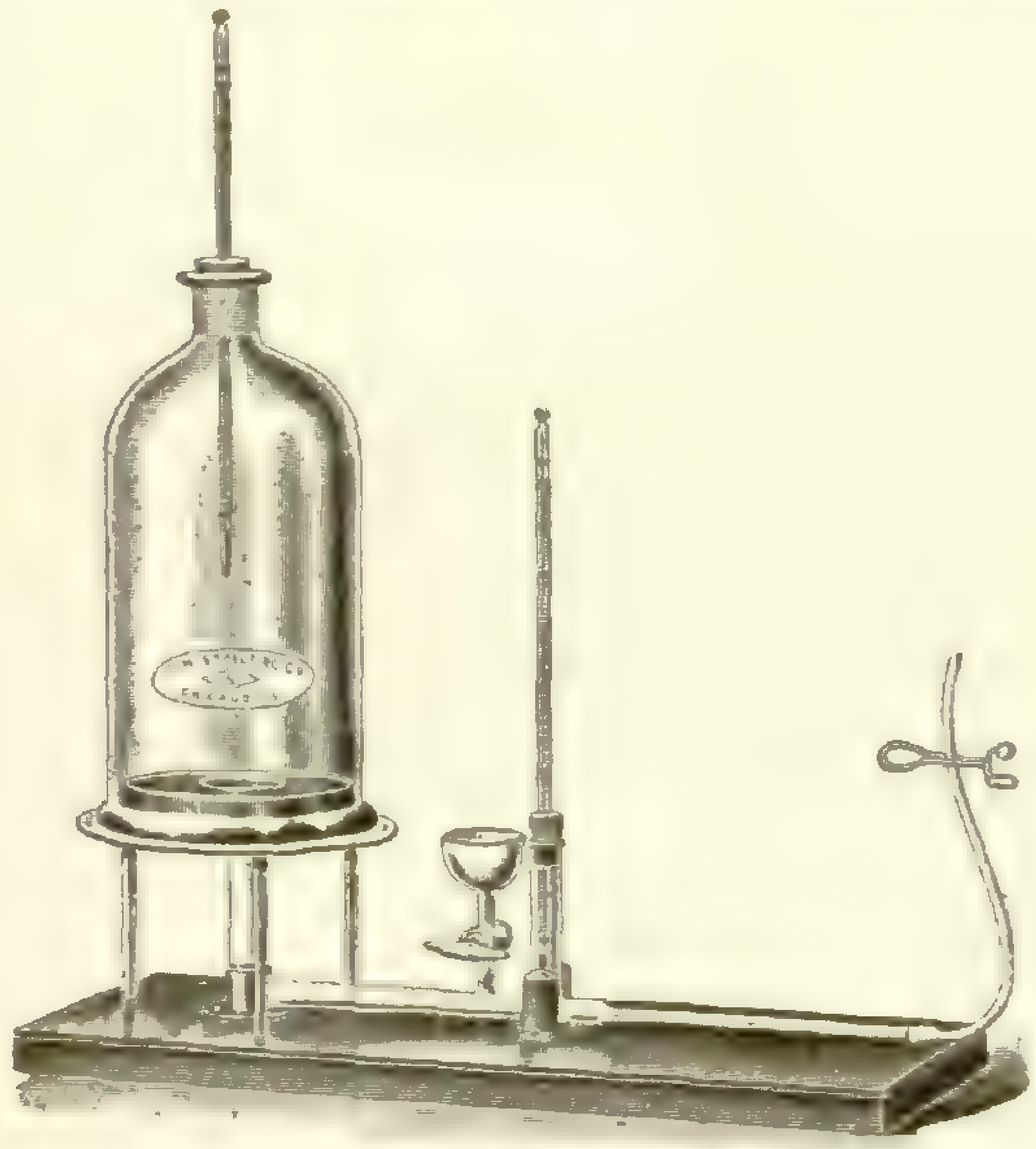

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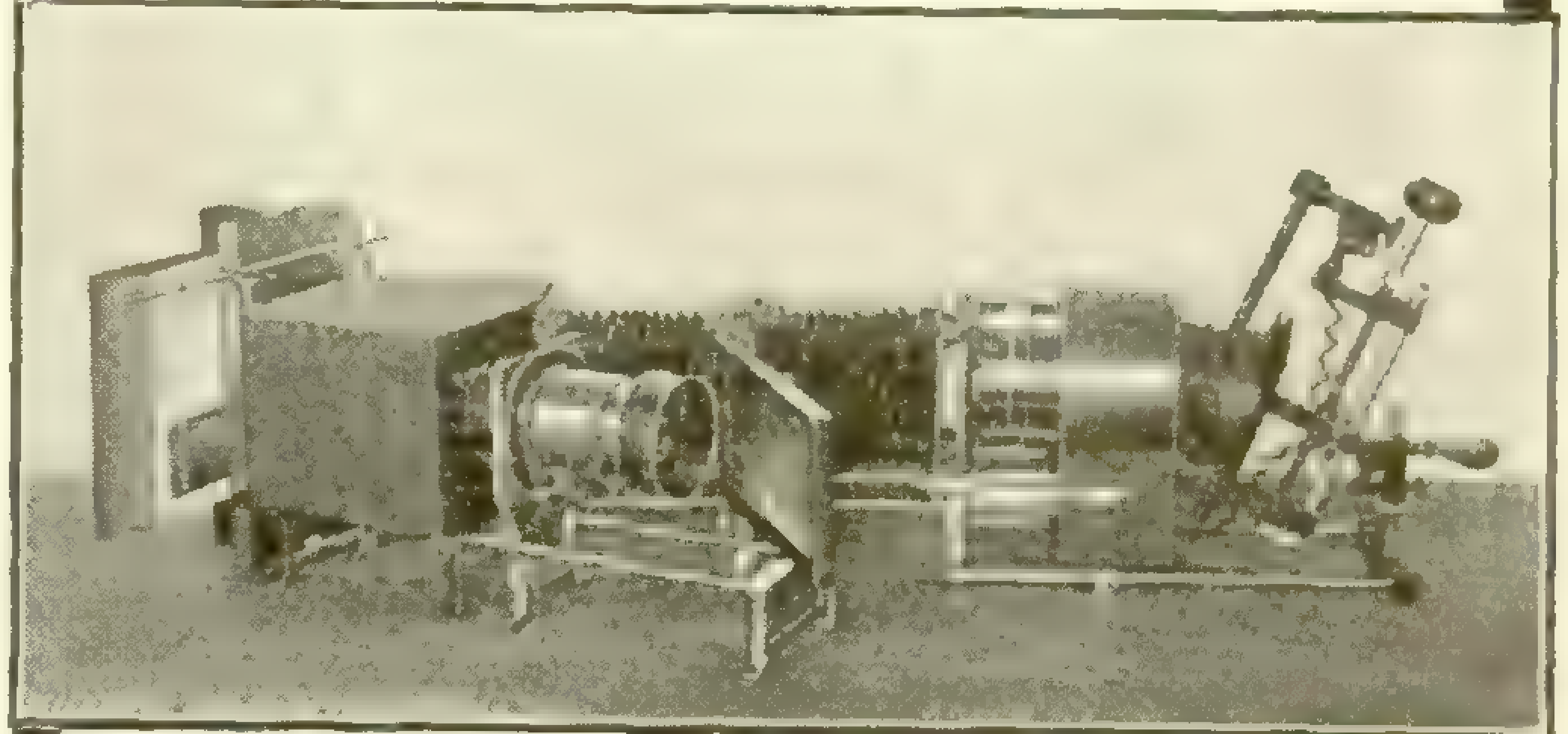

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VOLUME XLIV NUMBER 2

BOTANICAL GAZETTE

AUGUST 1907

THE ALTERNATION OF GENERATIONS AND THE MORPHOLOGY OF THE SPORE FORMS IN THE RUSTS

A. H. CHRISTMAN

(WITH PLATE VII)

DEBARY (**8**) was the first to establish the doctrine of heteroecism and explain the relationships between the fructifications occurring in a complete life-cycle of a rust having all of the spore forms. He first proved by inoculation experiments that sporidia from teleutospores of *Puccinia graminis* Pers. when sown on the barberry produce there the spermagonia and aecidia, and further that these aecidiospores taken from the barberry will again produce infections upon wheat.

In case of rusts which do not show a complete series of these spore forms it has been supposed and is still assumed to some extent that the missing stages exist, but are simply unknown in their correct relation to the known spore forms. But the methods of cross-infection, first successfully used by DEBARY (**8**, **9**), have led to the solution of many of the problems so far worked out in the life-cycle of the rusts, and by suitable infection experiments it has been established that one or more of the spore stages found in rusts with a complete life-cycle of the *P. graminis* type are regularly lacking in certain other rusts.

The question of the nature of the life-history in the *-opsis*, *brachy-*, *hemi-*, *lepto-*, and *micro-* forms, with their abbreviated cycles, has become of special importance since the discovery of sexuality and alternation of generations in the rusts. When comparing the complete life-cycle of a form like *Phragmidium violaceum* with that of *Phragmidium potentillae canadensis*, in which the aecidium is lacking, the question at once arises whether forms with a less number of spore types are to be considered as primitive and incomplete and in the process of developing into the conditions in *Eupuccinia*, or whether they are reduced and degenerate types. This question can be settled only on the basis of a complete morphological analysis of all the spore forms in question, and the following studies were undertaken as a contribution toward this end.

The most varied morphological interpretations have been given for each of the spore forms of the rusts, and it is worth while to summarize briefly the literature from this standpoint.

DEBARY'S (**10**) interpretation of the relations of the spore forms, given more than twenty years ago, has been recognized by many even to the present day as authoritative. He says: "The development of the aecidium-forming Uredineae agrees so nearly with that of the typical ascomycetes that certain stages in each group may be regarded as homologous with one another, though it must be allowed that the proof of the homologies is not quite perfect." The description of the formation of the aecidium cup is given somewhat as follows: The earliest stages consist of a tangled weft of hyphae. These enlarge, forming a dense mass which has the appearance of pseudo-parenchyma. This mass corresponds very well to the perithecium of certain ascomycetes. The hymenial cells appear at the base of this mass. From these club-shaped "basidia" the spores are abstricted to form rows. In his theoretical discussion DEBARY suggests the possibility of the hymenial layer having its origin in some large central female organ at the base of the aecidium. He was unable, however, to harmonize this view with what was known of the caeoma type of the aecidium.

In 1888, MASSEE (**18**) figured and described a peculiar organ occurring in the aecidium of *Uromyces poae* Rab. He made sections of the infected leaves of *Ranunculus ficaria*, and these sections were kept alive and studied as the processes went on. MASSEE found a large club-shaped branch at the base of the future pustule. A smaller antheridial cell was formed near by and fused with this oogonium, but the union was not clearly made out. The antheridium became empty and dwindled, while the oogonium became large and dense and nodules budded out upon its surface. These nodules elongated and formed the "basidia" from which the rows of aecidiospores are abstricted. Those nodules formed near the base of the oogonium produced the peridium. Before the fusion he finds in the oogonium, on staining with methyl green, a well-defined nucleus. After the union with the antheridium, MASSEE observed several small nuclei in this organ. As to the nuclei of the nodules he gives us no data. This account of the origin of the aecidium would lead naturally to the conclusion that the aecidium cup is a unit structure arising from a single fertilization. In that respect it would be perfectly comparable to the ascocarp.

ROSEN (**23**) in 1892 gave quite a different account of the formation of the aecidium in the case of *Uromyces pisi* Pers. In this form the end cells of the hyphae which bear the spores become much enlarged and at first contain one nucleus. This divides and the two so formed lie in the vertical axis of the cell. The one nearer the apex of this "basidium" divides to form two, and the portion of the cell containing them is separated off by the formation of a wall. This leaves the "basidium" containing one nucleus and the process may be repeated. ROSEN gives no account of a central organ from which the hyphae bearing the "basidia" arise. In the absence of such an organ the argument that the cup is the unit structure loses force. This would be even more markedly true if the same account of spore formation were found true for the aecidia of the caeoma type.

A year later DANGEARD and SAPPIN-TROUFFY (**7**) published an account of work done on the aecidia and also the teleutospores of various rusts. They interpret the fusion of the nuclei occurring in the teleutospore as being a fertilization and give to the process the name *pseudofécondation.* They regard the mature teleutospore as a fertilized egg and attach little significance to the origin of the binucleated condition. SAPPIN-TROUFFY also made some observations upon the spore-formation in other stages of the rusts. In the teleuto pustules of *Gymnosporangium sabinae* he found that one of the two nuclei of the "hymenial cell" enters the bud. A wall separates the bud from the basal cell, after which the single nucleus divides. These two nuclei now lie side by side in the bud and a simultaneous division occurs. A cell wall is then formed which separates the top or spore cell from the pedicel. SAPPIN-TROUFFY (**25**) later describes a similar budding in the uredospore pustule of *Uromyces betae* Pers. The process is the same except that a conjugate division of the two nuclei in the basal cell provides two nuclei for the young bud, instead of the basal cell sending one of its two nuclei into the bud. In my opinion it is altogether likely that the nuclear behavior in *Gymnosporangium sabinae* is the same as that described for *Uromyces betae.* In connection with his account of *Uromyces betae*, SAPPIN-TROUFFY points out the morphological likeness between the intercalary cell of the aecidium and the stalk cells of the uredospores. SAPPIN-TROUFFY (**25**) also shows that the cell at the base of the row of aecidiospores remains binucleated during spore-formation. The nuclear phenomena found in *Uromyces erythronii* DC. are different from those described by ROSEN. The two nuclei which normally lie irregularly placed in the end cell of the "sporiferous filament" come to lie side by side just before division. Simultaneous division of the two nuclei provides two nuclei for the cell which is to be separated off and leaves two to remain in the end cell of the hypha. SAPPIN-TROUFFY finds that in a great many rusts the binucleated phase has its beginning in these end cells. In his account there is no mention made of a large central organ such as was described by MASSEE. His observations, like ROSEN'S, would indicate that the rows of spores are perfectly independent structures.

POIRAULT and RACIBORSKI (**21**) gave a similar account of the behavior of the cells at the base of the aecidium. They believe that a single spindle is formed in the process of conjugate division, and with the work of SAPPIN-TROUFFY mentioned above have established quite satisfactorily that the two nuclei of the cells of the uredo and teleuto stages have each a distinct line of ancestors dating back to the basal cell of the aecidium at least.

In 1896 RICHARDS (**22**), working on *Uromyces caladii* Farl., found a large hypha, which he called the fertile hypha, at the base of the young aecidium. This hypha gives rise to several short branches, on the ends of which are borne the rows of spores. The "basidium," as he calls the end cell of one of these short branches, contains two or more nuclei; one migrates to the apex and there divides. The portion of the "basidium" which contains the two nuclei is separated off by a wall. RICHARDS' observations on nuclear behavior are of rather uncertain value, since he believed that all parts of the aecidium, including the vegetative mycelium, contained binucleated cells. He describes the same general method of aecidium-formation for the aecidia on *Houstonia caerulea* and *Ranunculus septentrionalis*. The process here described shows a marked resemblance to that found by MASSEE. There is a large hypha, which may be the outgrowth from a sexual cell or may have so originated in the ancestors of the rust.

MAIRE (**16**), in 1900, found in *Endophyllum sempervivi* Alb. & Schw. that the vegetative hyphae consist of uninucleated cells to their very ends in the base of the aecidium. These end cells, however, enlarge and become binucleated by a nuclear division unaccompanied by a cell division. Upon this binucleated end cell the spores are borne. MAIRE holds this process to be quite universal in the aecidium. In another paper (**17**) published about the same time, MAIRE compares the life-history in the Uredineae with that of the mosses and ferns and of cyclops. He sees in the beginning of this binucleated phase in the life-cycle the change from gametophyte to sporophyte, and in the fusion of the nuclei in the teleutospore a "mixie," while in the germination of the teleutospore and in the promycelium there occur the reduction divisions. The doctrine of alternation of generations in the development of the rusts, while opposed in essential points to the views of DANGEARD and SAPPIN-TROUFFY, has found confirmation in the later work of BLACKMAN and myself.

BLACKMAN (**2**) in 1904 was perhaps the first to show that two cells are concerned in the production of the binucleated cell at the base of the row of aecidiospores. In *Phragmidium violaceum* Wint. he found a series of large uninucleated cells standing vertically beneath the epidermis of the host. Each cell cuts off a sterile apical cell and then becomes binucleated by the entrance of a nucleus from one of the neighboring vegetative cells. This nuclear migration is accomplished by the smaller nucleus from the vegetative cell penetrating the wall by drawing itself through a small perforation. BLACKMAN terms this cell containing the two nuclei the fertile cell, and from it the row of spores and intercalary cells is produced. BLACKMAN agrees with

MAIRE in his general conclusions regarding the chromatin fusion and reduction in the maturing and germination of the teleutospore. He further believes that the entrance of the vegetative nucleus is to be interpreted as a fertilization, though describing it as a "reduced fertilization" which has replaced a former fertilization by a true male cell—the spermatium.

Shortly after the appearance of BLACKMAN'S paper, I described (5) a true fertilization in a somewhat similar form—*Phragmidium speciosum* Fr. The method of union of the two cells was found to be decidedly different. The cells combining are of approximately equal size, as are also their nuclei. Two such cells come together at some point on their adjacent walls. A considerable portion of the walls in contact dissolves away and the two protoplasts fuse. This large structure now elongates and from its apex a row of spores is abstricted (*fig. 18*). The same general behavior of the cells was found to occur in the aecidium of *Uromyces caladii*. Here, however, the cell produced by the fusion of the gametes elongates to a greater extent than in *Phragmidium speciosum*, and the two nuclei wander out into the elongated portion and remain there during spore-formation. The two bases of the gametes are often nearly obliterated. On the basis of these facts it was suggested that the rusts were after all more closely related to the lower fungi than to the red algae and ascomycetes. Certainly the union of the two cells is very like the zygospore formation common in the lower forms.

BLACKMAN and FRASER (3) in 1906 confirmed BLACKMAN'S previous observations on nuclear migration, this time working on the aecidium of *Uromyces poae* Rab. As described for *Phrag. violaceum*, they found that the nucleus migrates through the cell wall. Similar migrations were found in the aecidium of *Puccinia poarum* Niels.

In the aecidium of *Melampsora Rostrupi* Wagn., distinct evidences were obtained of the fusion of two large equal cells. In *Puccinia malvacearum* Mont., *Puccinia adoxae* DC., *Uromyces scillarum* Wint., and *Uromyces ficariae* Lév., BLACKMAN was unable to locate the origin of the binucleated phase. He suggests that a nuclear migration occurs in the hyphae some time between the infection with sporidia and aecidiospore-formation.

Still later (1907) I have described (6) a fusion of cells similar to that previously described for *Phrag. speciosum* and *Uromyces caladii*, but occurring in the formation of the primary uredospores of *Phrag. potentillae canadensis* Fr. The conditions here resemble those in *Uromyces caladii* more closely in that the nuclei leave the bases of the original gametes and come to lie in a very much elongated outgrowth of the fusion cell (*fig. 19*). The first cell is separated off from this basal cell much as it is in the typical aecidium. This cell divides into a spore and into the smaller sterile cell, in the aecidium known as the intercalary cell. Here this sterile cell elongates to form a stalk upon which the spore is borne. A second spore and stalk are formed beside the first by the pushing-out of a bud which is separated from the basal cell by a wall. This cell is formed into a spore and stalk cell in the same manner as was the first. These observations confirm most positively WINTER'S (**27**) suspicion that the primary uredo represents the aecidium of the *Brachypuccinia* forms and suggest further the morphological likeness between the stalked spores and those which are borne in rows and are separated by intercalary cells.

The earlier writers were plainly of the opinion that the aecidium cup had its origin in a single sexual organ, in which case apparent homologies between the aecidium cup and the ascocarp were conceivable. The existence of a fusion at the base of a cup from which the spore-bearing hyphae arise is still not established. Even if established it would leave the development of the caeomas unexplained. All later work has shown the rows of spores to be independent of one another in their development, both in the caeomas and in the cuplike aecidia. There can be no question that there is an apparent morphological equivalence between a row of spores of the caeoma and a row of spores in the aecidium cup. That being the case, it would appear that the latter is simply a more compact and protected condition inclosed within the peridium. It is plain that this peridium is not to be compared with the perithecial wall of the ascocarp, since the latter is purely gametophytic, being an outgrowth from those hyphae which bear the gametes. The peridium of the aecidium cup is well known to consist of rows of abortive spores and hence is sporophytic. The sterile mass of cells, which DEBARY compares with the perithecium and which appears before the hymenium is laid down, is perhaps comparable to the sterile cells which are cut from the gametes in the caeomas just before the conjugation. From the closely built structure of the aecidium cup it would not necessarily follow that the structure is developed from a single organ, since we have uredospore pustules in the Coleosporiums, which, without having a peridium, are quite as compact as are the aecidium cups of such a form as *Uromyces caladii*, and no sexual process can be assumed to have occurred in their origin.

As a foundation for a correct morphological interpretation of these various spore forms, I have undertaken a careful study of the development of those spore types which do not originate in a fusion cell.

UREDOSPORES

The secondary uredospores of *Phragmidium potentillae canadensis* are especially interesting because of their general resemblance to the primary uredospores which arise from a fusion cell as I have described (**6**). The secondary uredospores also arise from a large basal cell which contains two large nuclei. The basal cell here is borne upon a mycelium of binucleated cells (*fig. 1*). No fusion occurs in its formation, but it is plainly the equivalent, in its mature condition, of the so-called "basidium" of the aecidium cup which arises from a fusion cell. The two nuclei of the basal cell divide by conjugate division, and the pair of daughter nuclei lying in the distal portion of the basal cell are separated off by a cross wall, thus forming the first spore-initial cell. A further conjugate nuclear division, followed by a cell division, at once separates this initial cell into a spore and a smaller cell below, which elongates to form a stalk upon which the spore is borne (*fig. 2*). About the time the first spore is formed, a bud appears on the basal cell beside the stalk of the first uredospore (*fig. 3*). A second simultaneous division of the nuclei of the basal cell provides this bud with two nuclei, leaving two in the basal cell. A wall now separates off this second uredospore-initial cell (*fig. 4*). It in turn divides, forming a second spore and stalk in the manner described for the first (*fig. 5*). In the same manner a third spore is produced (*fig. 21*).

On comparing these figures with the ones given in my description of spore-formation in the primary uredo (**6**) of this same rust, the striking likeness is at once apparent. The only difference lies in the method of formation of the basal cells and in the binucleated condition of the vegetative mycelial cells from which they arise. The primary uredosorus arises from a mycelium of uninucleated cells (*fig. 6*), while the secondary uredosorus arises on a mycelium with regularly binucleated cells (*fig. 1;* compare *figs. 19* and *21*).

Like the secondary uredospores of *Phragmidium potentillae canadensis*, the uredospores of the Coleosporiums are borne upon a mycelium of binucleated cells. On this mycelium large basal cells are formed in the same way as in Phragmidium. When the spores form, however, as figured and described by HOLDEN and HARPER (**4**), the second uredospore-initial cell is cut off directly beneath the first spore and intercalary cell. This is repeated in the case of the following spores, and a row of uredospores separated by intercalary cells is formed, having exactly the appearance of the rows in the true aecidium (*fig. 20*).

Uredospores are generally unicellular, but, as ROZE (**24**) and later JACKY (**15**) have shown, the uredospores of *Puccinia chrysanthemi* are quite commonly two-celled.

TELEUTOSPORES

I have studied in detail the formation of the teleutospores of *Puccinia podophylli* S., and a similar series of cell phenomena to those described for the secondary uredospore of *Phragmidium potentillae canadensis* is to be observed here. A series of large binucleated cells is formed beneath the epidermis of the host. These cells are the ends of hyphae which are made up entirely of binucleated cells and are in position and general appearance exactly like the basal cells of the uredosori, and like those cells bear the spores. Conjugate nuclear division followed by cell division now separates off a large distal cell or teleutospore-initial cell (*fig. 7*). As in the case of the uredospore, this cell now divides to form the spore and the stalk (*fig. 8*). In the genus Uromyces the teleutospore remains unicellular. Here, however, like the uredospore of *Puccinia chrysanthemi*, this one cell divides to form the characteristic two-celled spore of the genus Puccinia. As is well known in Triphragmium and Phragmidium, three and four-celled spores are produced from a single initial spore-cell. It is plain that this multiplication of cells in the teleutospore increases the number of sporidia produced and so increases the chances of infecting the aecidium host the following spring. The developmental stages in this case were worked out in greater detail in connection with the formation of the second spore produced from the basal cell. About the time the cell division for the formation of the first spore is complete, a hyphal bud is pushed up beside the stalk of the first spore. A nuclear division occurs in the region of the neck of this bud (*fig. 9*). The spindles are here so placed that there can be no question but that a daughter nucleus from each of the nuclei of the basal cell will enter the bud, while the other two daughter nuclei will remain in the basal cell. The bud is separated from the basal cell by a wall, thus forming the second teleutospore-initial cell. A simultaneous nuclear division follows within this cell (*fig. 10*), and a cell wall cuts off the spore cell and the stalk cell. That it is the upper one of these two cells which produces the two cells of the teleutospore is shown in *fig. 11*, where the cell wall is just forming. A third bud is formed at about this time and a third spore is produced in the same manner as has just been described (*fig. 12*).

While at work on the teleuto stage of *Puccinia podophylli* a further interesting phenomenon was observed. The occasional occurrence of trinucleated cells, together with BLACKMAN'S account of migrations of nuclei among vegetative cells in *Puccinia poarum*, suggested that possibly nuclear migrations occur in the fungi, as well as in the higher plants, as purely pathological phenomena.

MIEHE (**19**) has shown that when the epidermis is stripped from the leaves of *Allium nutans* the nuclei of certain cells become pointed and finally a thin beak penetrates the wall into a neighboring cell. The portion of the nucleus which has passed the wall enlarges to form a highly refractive, densely staining vesicle. This vesicle increases in size as the nuclear material finally passes over into the foreign cell. MIEHE has found cells containing as many as five nuclei as a result of such migration. The explanation given is that the condition is a pathological one in which the nuclei migrate as a reaction to the wound inflicted in removing the epidermis.

SCHÜRHOFF (**26**) found essentially the same phenomena occurring in *Iris germanica*. He also mentions the formation of the vesicle which has a marked affinity for the red of the triple stain.

A careful study of the teleutosori of *Puccinia podophylli* revealed that nuclear migrations are quite common here. This was particularly true at the base of the spores and in the margins of the sori. The nucleus forms a beak which penetrates into a neighboring cell (*fig. 13*). This projection elongates, forming a sort of thread as the material of the nucleus passes over into the foreign cell (*fig. 14*). At this stage the elongated portion of the nucleus loses its normal structure and becomes densely stained with the red of the triple stain. This dense staining is figured by MIEHE and SCHÜRHOFF, and appears in figures by BLACKMAN. The portion of the nucleus which has passed the wall now begins to enlarge (*figs. 15, 16*). In the latter figure there is evidence that the nucleus migrates from one cell of a hypha to the next, while in the other cases the nuclei appear to be migrating from one hypha to another.

Sections which show all the nuclei of the cells concerned in the migration are hard to obtain. By studying the series of sections to which *fig. 14* belongs, it was found that cell *a* contained two nuclei, while cell *b* contained but one. From this it seems plain that in this case there is a migration between normal vegetative cells of the sporophyte where no fertilization can be assumed. This would result in the production of a cell with three nuclei. Indeed this condition is quite common (*fig. 17*).

The only interpretation possible here seems to be the one given by MIEHE, that this condition is entirely pathological and possibly due to the wound produced at the time of fixation. The fact that three- and four-nucleated spores are often found has been pointed out by SAPPIN-TROUFFY and BLACKMAN. If such spores result from pathological nuclear migration, this would indicate that the pathological condition which produced the migration must have occurred a considerable time before fixation, which is hardly an adequate hypothesis. The wounding in preparation for the killing solution perhaps explains well enough figures in which the nuclei are in process of migration. The fact that the migrations were observed in many cases in a sort of rudimentary paraphysis bounding the pustules is perhaps significant. It undoubtedly helps to explain certain conditions in the cuplike aecidia where isolated binucleated cells are often found in the older pustules quite out of range of the bases of the rows of spores where the fertilization processes occur.

MORPHOLOGICAL DISCUSSION

It cannot be decided, perhaps, on the data at present available whether the fusion at the end of the uninucleated generation is of a primary or secondary nature and origin. There can be no question, however, that it is physiologically the fertilization stage in the development of the rust, and that it is the beginning of a sporophyte generation which ends with the reduction divisions in the germinating teleutospore, as described by MAIRE (**16**, **17**) and later by BLACKMAN (**2**). HARPER (**13**) has also argued, on the data given by BLACKMAN and myself, that an essentially similar alternation of generations is found in the rusts to that in the ascomycetes and red algae. The existence of well-defined gametophyte and sporophyte stages in these forms can no longer be questioned.

If we take up the cases of the aecidio-, uredo-, and teleutospores in the light of the facts above described, it is plain that we have in the successive production of these forms a series of asexual reproductive cycles within the sporophyte generation. In thus showing a series of subgenerations, each ending with a particular spore form, which taken together compose the sporophyte, the rusts are unlike any other group of plants in which true alternation of generations is known.

The essential characteristics of these subgenerations is that in each case they begin and close with the peculiar structure first described and long known as "basidium," or, as BLACKMAN has pointed out, better called the basal cell. This is the morphological unit, whose correct interpretation gives the key to the explanation of the puzzling and hitherto unexplained reduplication of forms which is at once the most conspicuous and least understood feature of the entire group.

With the establishment of the identity of the basal cells of the uredosori and teleutosori with one another and with the basidium of the aecidium, and the interpretation of this cell in the aecidium as the primitive spore-producing cell of the sporophyte generation of the rusts, the morphology of such diverse and puzzling structures as aecidio-, uredo-, and teleutospores and stalk and intercalary cells becomes at once clear.

Considered from this point of view, we find the gametophyte generation consisting of a mycelium of uninucleated cells, beginning with the sporidia and ending with the fusion of two gametes, and bearing asexually one kind of spores, the so-called spermatia. The question as to how the so-called secondary aecidia arise must be regarded as still unsettled. DIETEL (**11**) has shown that infections from aecidia in the case of *Uromyces scrophulariae* DC. may reproduce crops of aecidiospores. In this case one or more of three things may have taken place: the infecting aecidiospore may have germinated by the formation of a sort of promycelium and sporidium, thus returning to the uninucleated condition, as is the case in Endophyllum; or these secondary aecidia may be borne upon a mycelium of binucleated cells, in which case they are not aecidia at all, but rather uredospores borne in rows such as occur in Coleosporium; or spermatia capable of producing infection may accompany some of these forms having the secondary aecidia.

Against this last view we have the present belief that the spermatia are functionless, a belief which in view of the great number of forms to be studied is certainly open to some question, especially since BREFELD (**4**) and PLOWRIGHT (**20**) claim to have seen distinct evidences of normal germination in the spermatia of *Puccinia graminis*, *Uromyces pisi*, *Puccinia tragopogonis*, *Puccinia coronata*, and others. This is a behavior quite unlike what might be expected of true spermatia. In my opinion, the likeness of the rusts to the red algae is very questionable, and the arguments that the spermatia are the former male cells are none too convincing. I incline rather to the view that spermatia represent the once functional asexual spores of the gametophyte. This view finds support in the fact that they are in general appearance very like the functional asexual spores (pycnidia) of the gametophyte of certain ascomycetes; also in structure and general appearance they are very like the other gametophytic spores of the rusts, the sporidia, which are still functional; further, unless we interpret the spermatia as the asexually produced gametophytic spores, the gametophyte generation is left entirely without means of reproducing itself without passing through the stages of the sporophytic generation. As yet, however, it must be admitted that definite evidence as to the nature of the spermatia is very incomplete.

The binucleated sporophytic generation which, as MAIRE (**17**) has pointed out, is comparable to the generation with the double number of chromosomes in the higher plants, has its beginning in the cell produced by the fusion of two gametes—the fusion cell. This cell produces a more or less elongated outgrowth which has been long known as the "basidium," and has been often figured and fully described. For obvious reasons, that BLACKMAN has pointed out, the term basal cell is to be preferred to the old term basidium. This cell now produces spores, being a generative cell. The spores may be borne in chains, as has been so often described for the true aecidia, or they may be produced by a process of budding and so be borne on stalks, as I found to be the case in the primary uredosori (*figs. 18, 19*).

The spores produced by this first basal cell may infect the same host upon which the gametophyte is parasitic, or they may infect some other host and produce there a sporophyte mycelium. After a period of development this mycelium fruits. When spores are to be produced, large binucleated cells—the basal cells—in all essentials like the cells upon which the aecidiospores and primary uredospores are borne, again appear, this time upon the ends of the binucleated hyphae which mass together beneath the epidermis to form the uredosorus. By a process of cell division above described the uredospores are formed. These uredospores may be borne in rows and separated by intercalary cells, as in the case of Coleosporium, or they may be borne upon stalks, as described above for *Phragmidium potentillae canadensis*. The uredospores may reinfect the same host or hosts and repeat this generation an almost indefinite number of times, as is commonly supposed to be the case in *Puccinia rubigo-vera*.

Usually, after a few generations of uredospores have been produced, the binucleated mycelium bears the teleutospores which are to end the sporophytic phase in the life-cycle. When teleutospores are about to form, end cells of the hyphae again return to the condition of the large basal cell, and the teleutospores are budded off exactly as are the primary and secondary uredospores. At present we know of only one form in which the teleutospores are borne in chains and separated by intercalary cells. Another approach to this condition is perhaps found in the sessile teleutospore of Melampsora and Coleosporium. The teleutospores of the different genera are only secondarily characterized by being made up of one to several cells.

The bearing of these facts upon the problems of classification presented by the rusts is of primary importance. Assuming the existence of alternation of generations, there can be no doubt that the gametophyte is to be regarded as the primitive, original generation. The autoecious rusts are probably to be regarded also as more primitive than those which are heteroecious. It is most suggestive of the truth of this view that the rusts show alternation of generations at the time the change from one host to another occurs. Older schemes of classification of course have left all such considerations out of account.

SCHROETER has classified the rusts on the ground of the various types of spores occurring in the life-histories of the different forms. To him we are indebted for the convenient separation into *eu-*, *-opsis*, *brachy-*, *hemi-*, *micro-*, and *lepto-* types. Obvious difficulties arise with this classification as used up to the present time. Assuming all primary uredospores to be in reality aecidiospores, as is the case in *Phragmidium potentillae canadensis*, would at once throw all of the *brachy-* and *hemi-* forms into the *Eupuccinia* class. If we retain the term *Brachypuccinia* on the ground of the primary uredospores having stalks, to be consistent it would be necessary to class Coleosporium with the *-opsis* forms, since its uredospores are borne in rows as are aecidiospores.

DEBARY (**10**) made his first division in the group by separating the aecidium-forming rusts from the so-called tremelloid forms. He regards the former as being homologous in essential details with the ascomycetes, and points out that the tremelloid forms may be regarded as either more primitive and in process of being developed, or reduced forms produced by the modification of the aecidium-bearing forms. It is plain, however, that with our present knowledge no such division is to be considered. As I have pointed out, the primary uredo is morphologically an aecidium. Further, Dr. OLIVE permits me to quote results, not yet published, which show that the teleutospores of *Puccinia transformans*, a *micro-* form, are borne upon basal cells which are the outgrowth of a fusion cell produced upon a mycelium having uninucleated cells. There are then teleutospores which in their origin are the same as the aecidiospores and primary uredospores, and this argues very strongly that the stage with uninucleated cells is to be regarded as always present.

ARTHUR'S (1) new classification is based upon the assumption that all of the spore forms—*spermatia*, *aecidio-*, *uredo-*, and *teleutospores*, and *sporidia*— were present in the ancestors of our rusts, and he leaves untouched the question of the origin of this multiplicity of spore forms. Reasoning from this assumption, the forms with abbreviated life-cycles arise by a process of elimination. In this way any portions of the sporophyte and perhaps the whole gametophyte might be successively suppressed.

Endophyllum has perhaps arisen in this way. In it a uninucleated mycelium produces binucleated aecidiospores which apparently have no uredo host. The spores germinate by a sort of promycelium which bears four uninucleated sporidia. These sporidia again infect the aecidial host, producing again a mycelium of uninucleated cells.

If we assume on the other hand that the rusts evolved from lower fungi, and that the various subgenerations of the sporophyte are being added and intercalated, as well as perhaps in some way old forms eliminated, quite a different classification is suggested. The gametophyte is universally regarded as the primitive generation, and in its earliest appearance was relatively simple. In the pteridophytes the sporophyte increases in importance until the gametophyte is finally the more inconspicuous.

I incline to the view that the *lepto-* and *micro-* forms, in which the teleutospores or spermatia and teleutospores only occur and are borne on mycelia with uninucleate cells, are the primitive rusts. We have in them the gametophyte bearing the gametes and producing the fusion cell. A very short outgrowth of this cell now bears the teleutospores in which the sporophyte generation has its end. The first modification of this life-history would then appear in a further development of the sporophyte. This might be brought about by the fusion cell producing a mycelium directly rather than the basal cell normally produced, or it is possible that the basal cell should produce temporary spores, which might carry this sporophytic mycelium to other tissue, a result which would be altogether favorable on account of the exhausted condition of the host in the neighborhood of the fusion cell. Spores formed in this way would conform to our definition of primary uredospores, which it would thus appear are to be considered as the first added spore generation, and the *brachy-* form would thus be the first derived type. With such a first crop of temporary spores once formed, it is easy to see how they might be formed in successive crops—the secondary uredospores—before the teleutospores are finally formed and the sporophytic generation closed.

A modification of the stalk cell with loss of essential function would result in the formation of the true aecidium. The short intercalary cells of the aecidium give us a decided argument for the belief that the aecidiospores are not the primitive spore type, since I am of the opinion that we can only regard the intercalary cell as practically a functionless cell. The argument that the intercalary cell is for the purpose of disjoining the spores is hardly tenable, since we have many fungi in which, as in Cystopus, chains of conidia are formed, the spores of which separate readily without alternating sterile cells. Looked upon as a rudimentary stalk, we can hardly assume that it is in process of progressive evolution, since from that point of view we would have the curious case of a functionless structure being first developed, to be modified later into a structure of some service to the plant. It is relatively common, on the other hand, to find that functional structures degenerate on becoming useless, becoming smaller and finally disappearing. The degeneration of the uredo stalk cell is doubtless correlated with the development of the spore pustule, resulting in the formation of the spores in chains instead of in a horizontal series. The spore-initial cells, which have in other cases divided to produce spores and stalk cells, still divide, forming the spore and the small intercalary cell, the degenerated representative of the former stalk cell. With the change from the stalked primary uredospores to the chains of aecidiospores, we have formed the typical autoecious *eu-* type of rust. If now the sporidia find a more favorable host in some other plant than that bearing the uredospores and teleuto spores, a later change of host for the sporophyte generation would explain heteroecism. It is certainly conceivable that the change of host should occur at the germination of the first-formed binucleated spore. Certainly the sporidia and the gametophytic mycelia produced by them are sufficiently different from the sporophytic aecidiospores and uredospores and the mycelia which they produce to explain such a change in some measure.

From either point of view it would appear that a heteroecious *eu-* form is the highest in complexity and a late stage in the development of the rusts. The peridium is undoubtedly a late modification for protection, and cuplike aecidia are very likely less primitive than the caeomas. This would argue that a rust of the *Puccinia graminis* type is in structure very far removed from the primitive rust, a view which is quite opposed to the stand taken by BLACKMAN.

I entirely agree with DIETEL (12) that the presence or absence of the secondary uredospores in the life-cycle is of secondary importance when considering the history of the rusts. The essential stages are those of cell fusion and chromatin fusion and reduction. The uredospores simply prolong the sporophytic phase as the conditions demand, and it is likely that the *-opsis* forms may result from the elimination of the uredo stage in some rusts; while in others they represent an earlier less complete stage in evolution than the *eu-* forms.

The curious condition found in Endophyllum may well have arisen by the elimination, for some cause, of the teleuto and uredo stages. The cuplike structure and short intercalary cells all point to its once having been a very highly specialized form from the standpoint of evolution. It is quite conceivable that as a result of some change in condition the aecidiospores should have developed the capacity to reinfect the aecidium host.

The facts of alternation of generations in the rusts are in harmony with DIETEL'S view that the *micro-* and *lepto-* forms are the most primitive types of rusts. Besides the arguments advanced above, we have in the diverse structures of the teleutospores of the different genera a further support for this view. Assuming the teleutospores to be the oldest spore form, it is easy to see how they might have become more markedly modified than the newer uredo- and aecidiospores. The loss of function of the spermatia as gametophytic conidia, too, is exactly what might be expected with the development of the sporophytic spores.

The writer wishes to acknowledge his indebtedness to Professor R. A. HARPER for his many helpful suggestions and other assistance, and also to Dr. E. W. OLIVE for permitting him to use the data concerning *Puccinia transformans* in advance of its publication by him.

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EXPLANATION OF PLATE VII

Figs. 1–17 were drawn with the camera lucida, using ocular IV and the $\frac{1}{16}$ oil immersion objective of Leitz. *Figs. 18–22* are semi-diagrammatic and the magnification has been adjusted to bring the figures of the different rusts to approximately the same dimensions on the plate.

Phragmidium potentillae canadensis

FIG. 1.—A portion of the mycelium showing the binucleated condition of the cells of the secondary uredo.

FIG. 2.—The first spore-initial cell dividing into spore and stalk cell.

FIG. 3.—An early stage in the budding-off of the second spore.

FIG. 4.—A fully formed second spore-initial cell.

FIG. 5.—The divisions forming the second spore and stalk have been completed; the stalk of the first spore is also shown.

FIG. 6.—A portion of the mycelium showing the uninucleated condition of the cells (compare with *fig. 1*).

Puccinia podophylli

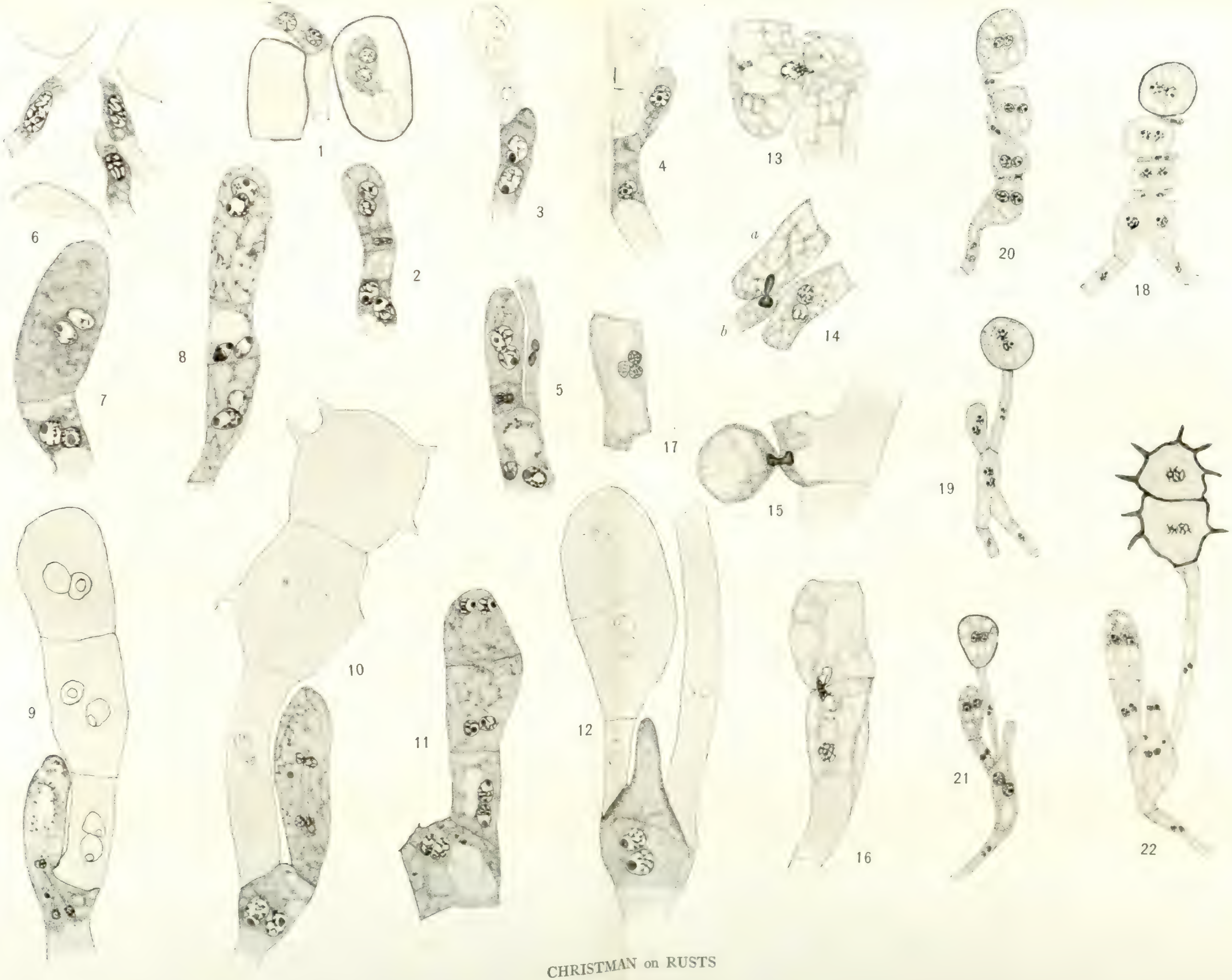
FIG. 7.—A stage showing the basal cell and the first teleutospore-initial cell.

FIG. 8.—The spore-initial cell has divided into a stalk cell and a larger distal cell which is to divide and produce the two-celled teleutospore (see *fig. 11*).

FIG. 9.—Simultaneous nuclear division supplying the second spore-initial cell with nuclei.

FIG. 10.—A second spore-initial cell showing nuclear division before division into stalk and spore.

FIG. 12.—A stage showing the division of the distal cell into the two cells the spore.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CHRISTMAN on RUSTS

FIGS. 13-16.—Various stages of nuclear migration in the mycelium of the teleutosorus.

FIG. 17.—A mycelial cell showing three nuclei.

Semi-diagrammatic figures

FIG. 18.—*Phragmidium speciosum.* Mycelial cells of the aecidium showing uninucleated cells bearing a fusion cell and the rows of spores and intercalary cells.

FIG. 19.—*Phragmidium potentillae canadensis*, showing uninucleated mycelial cells in the primary uredo similar to those in the aecidium; a fusion cell is formed in much the same way as in the aecidium; the elongated basal cell represents an outgrowth after fusion; here the spores are budded off as a horizontal series and are borne on stalks.

FIG. 20.—*Coleosporium solidaginis.* Uredospores borne in chains on a mycelium of binucleated cells.

FIG. 21.—*Phragmidium potentillae canadensis.* Secondary uredospores budded from the basal cell; the mycelium is composed of binucleated cells.

FIG. 22.—*Puccinia podophylli.* Teleutospores in various stages of formation; the cells of the mycelium each contain two nuclei.

DEVELOPMENT OF THE WALLS IN THE PROEMBRYO OF *PINUS LARICIO*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCVI

N. Johanna Kildahl

(WITH PLATES VIII AND IX)

HISTORICAL SKETCH

In 1862 Hofmeister (**1**) gave the principal facts in the development of the proembryo of *Pinus Strobus* and *Pinus Abies*, although he did not touch upon the development of the walls.

Strasburger (**2**) worked out the development of the proembryo in more detail in 1876, and he was the first to recognize the arrangement in tiers. He says that after the four free nuclei have reached the basal end of the egg, and arranged themselves into a plane, the nuclei opposite each other exert an influence upon the surrounding protoplasm, giving it a parallel-striped appearance, and that this influence is also exerted upon the protoplasm of the egg mass above the nuclei; a row of granules then appears upon the parallel stripes; at the metaphase of the first division, after the nuclei have reached the base of the spore, the stripes and row of granules toward the egg-mass disappear, while those between the nuclei persist, form membranes, and become the permanent vertical walls.

In 1898 Blackman (**3**), in describing the proembryo of *Pinus silvestris*, said that after the four nuclei have passed to the bottom of the egg they become surrounded by protoplasmic fibers which radiate from the nuclei into the cytoplasm; they have no definite arrangement, but are mostly directed away from the base of the egg. At a later stage, when the four nuclei have arranged themselves in one plane, the fibers also are confined to the basal end of the egg and form a mass in which the nuclei lie, the mass projecting a little above the nuclei; after this the two walls are formed at right angles to each other and to the base of the egg, so that each nucleus lies in one end of a shaft which is open toward the main mass of the egg; after the walls have been formed the fibers disappear. He says that he could not determine exactly what part the fibers play in the formation of these walls, but of their connection with them there can be no doubt.

The next work on Pinus was that of CHAMBERLAIN (**4**), who describes the four nuclei in moving toward the base of the egg as being invested by strong fibers which are directed tangentially. "Upon reaching the base of the oospore the four nuclei arrange themselves in a plane and become ensheathed by fibers derived from the nuclear membrane. Two walls are then formed at right angles to each other and to the base of the spore, each nucleus thus being separated from the others, but freely exposed to the general cytoplasm of the spore." He quotes BLACKMAN (**3**) as thinking that these fibers have some intimate connection with the formation of the walls, and thinks that the appearance of these first incomplete walls is quite apart from nuclear division.

In 1904 Miss FERGUSON (**5**) stated that "after attaining full size, the four nuclei pass to the base of the oosphere." "During their descent many fibers arise in the cytoplasm surrounding the nuclei," and she quotes BLACKMAN as suggesting a relation between these fibers and the walls that arise later, but says that she finds no connection between the two. In regard to the formation of the first walls she says: "During mitosis the deeply staining substance surrounding these nuclei condenses into large, irregular masses at the periphery of the nucleus. When the eight nuclei are formed this deeply staining material collects about them and extends in irregular strands into the cytoplasm. Each nucleus is now surrounded by its own cytoplasm, though no cell-walls have yet been laid down." Further, she says: "In the five species of pines which I have studied, cell-walls do not arise until after eight nuclei have been formed. The deeply staining cytoplasmic substance appears to be repelled from all sides of these nuclei and is deposited in lines which indicate the position of the future cell-walls; the cell-membranes appear to arise by a direct transformation of this substance."

DEVELOPMENT OF WALLS

The material for the following study of the development of walls in the proembryo of *Pinus Laricio* was collected during the summers of 1905 and 1906. It was taken from different trees and localities.

Preparations were also loaned to the writer by Miss LULU PACE, and preparations and material by Professor W. E. PRAEGER.

After the four nuclei have passed to the basal end of the egg, each nucleus is surrounded by a thick sheath of fibers, forming a sphere with the nucleus in the center; these fibers, according to CHAMBERLAIN, are derived from the nuclear membranes. The fibers next to the nuclei disappear first; where the sheaths come in contact, between the nuclei, they form a pseudo-wall, giving the appearance, under low power, of a vertical wall (*fig. 1*). It was this, no doubt, which was seen by the previous observers, STRASBURGER, BLACKMAN, and CHAMBERLAIN, and described by them as a vertical wall.

The cytoplasm surrounding the nuclei at this time is of a uniform granular consistency, with small vacuoles. When the first division of the four nuclei has reached the metaphase, every vestige of these fibers has disappeared (*fig. 2*). The spindles are blunt and broad, showing a tendency towards multipolarity, though considerable variation exists in the form of the spindles during this division. A marked change has taken place in the surrounding protoplasm, which has become charged with very coarse, deeply staining granules. In the early telophase these coarse granules still persist, but there is a larger clear space, filled with fibers, around each spindle (*fig. 3*).

In late telophase (*fig. 4*) the cell plate, from which the cross wall is formed, has been developed. The nuclear membrane has appeared, and above each daughter nucleus is a deeply staining granular area. Fibers radiate from the daughter nuclei in all directions and the coarse granules seem to be strung along the fibers and pushed away by them. The spindle fibers gradually disappear until they are visible only on each side of the cell plate, as is shown in *fig. 5*. The granular area surrounding each nucleus in *fig. 4* is now replaced by an area much more finely granular.

The formation of the vertical walls is begun at this stage. They begin at the cross walls and extend in both directions until they reach the base of the egg on one side, and extend somewhat beyond the nuclei on the other (*fig. 8*). These walls are undoubtedly formed upon secondary fibers, which can be seen coming together in *fig. 4*, and more distinctly in *fig. 5*, although no granules have yet been formed to show the position of the cell plate; these are shown distinctly in *fig. 9*. *Figs. 6* and *9* show the fibers radiating from the nuclei to the walls. The vertical walls in each tier are formed by the fibers from the nuclei of their respective tiers, as is shown in *fig. 8*. As a rule the cross wall is formed somewhat in advance of the vertical wall (*figs. 4–9*). *Fig. 8* shows the cross walls completed, except at the edges, while the vertical walls are still in an early stage of development; this is also shown in *fig. 9*. The cross walls are formed in the usual way, each on its own spindle, as is shown in *fig. 6*. These walls, therefore, are formed in connection with the first division of the four nuclei. It might be said that the proembryo passes from the four-nucleate stage to the eight-celled stage were it not for the fact that the four nuclei farthest from the base of the egg are still freely exposed to the egg mass.

The very coarse granules gradually disappear, as shown in *figs. 4–9*, while the deeply staining areas first seen in *fig. 4* increase in size until in *figs. 8* and *9* they entirely surround the nuclei and extend irregularly into the surrounding cytoplasm.

The second division in the base of the egg, as a rule, takes place in the exposed tier (*fig. 10*), although it may take place in the basal tier, as shown in *fig. 11*. The cross and vertical walls are formed as in the previous division.

The next and last division occurs in the basal tier (*fig. 12*), and, so far as has been reported, it never takes place in either of the other two tiers. This sequence of divisions is also reported by HOFMEISTER (**1**) in *Pinus Strobus* and by MIYAKE (**6**) in *Picea excelsa*. The last division in the proembryo of *Pinus Laricio* is not always simultaneous in the four nuclei, as has heretofore been reported; one section showed two nuclei in metaphase and the other two in late telophase.

The proembryo has now completed its development and consists of three completely walled tiers of four cells each, and the tier of four nuclei separated from each other by vertical walls but free toward the egg mass.

SUMMARY

1. The cross walls in the proembryo of *Pinus Laricio* are formed in the usual way, on cell plates formed on the spindles in the division of the nuclei, and the first cross walls come in a little in advance of the vertical walls.

2. The vertical walls in each tier are formed by the secondary fibers from the nuclei of their respective tiers.

3. The first cross walls and the first vertical walls are formed in connection with the division of the first four free nuclei at the base of the egg.

4. The second division in the basal end of the egg may take place in either tier.

5. In the last division the four nuclei do not always divide simultaneously.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES VIII AND IX

PLATE VIII

FIG. 1. Section showing fibers between nuclei that give appearance of vertical wall. ×225.

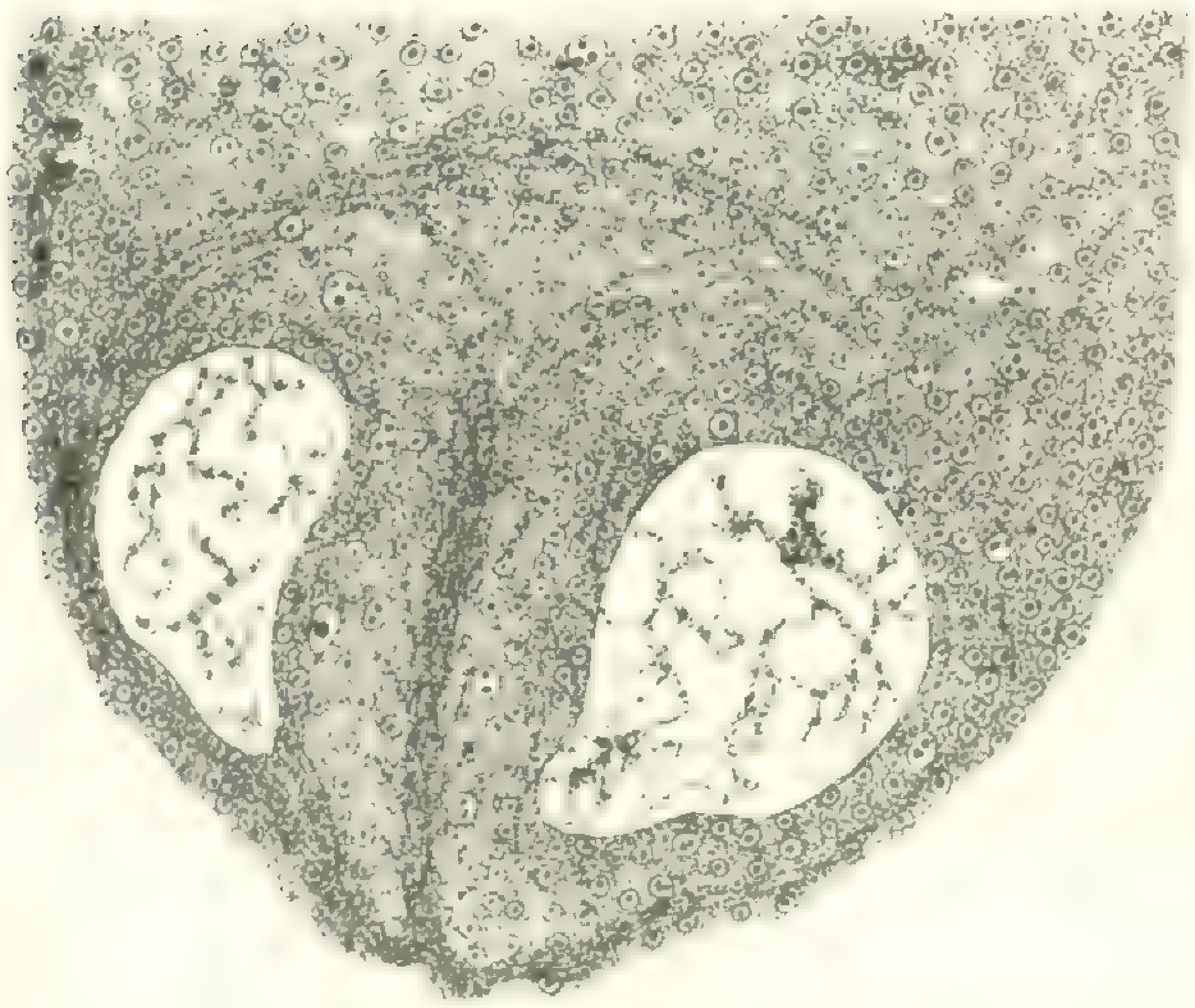
FIG. 2. Metaphase of first division, showing entire disappearance of fibers, blunt broad spindles, and coarse granular substance. ×610.

FIG. 3. Telophase of same division; fibers radiating in all directions; cell plate not yet visible. ×355.

FIG. 4. Appearance of cell plate; nuclear membranes; dark areas above daughter nuclei; fibers radiating from nuclei and coarse granules strung along fibers; secondary fibers coming together in the center, upon which is formed the vertical wall. ×390.

FIG. 5. Later stage in cross walls and beginning of vertical walls. ×365.

FIG. 6. Later stage in formation of vertical walls; fibers radiating from nuclei. ×390.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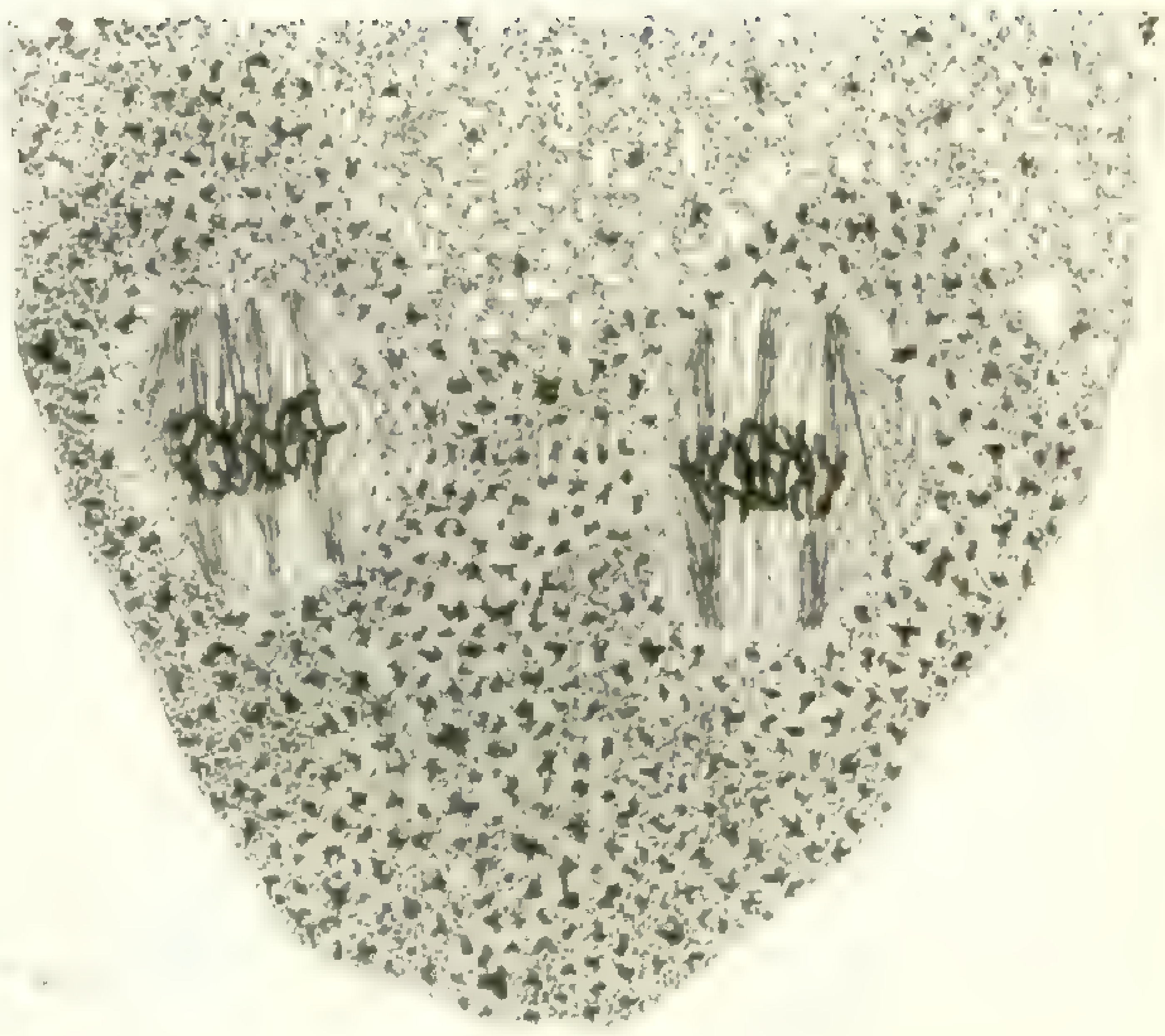
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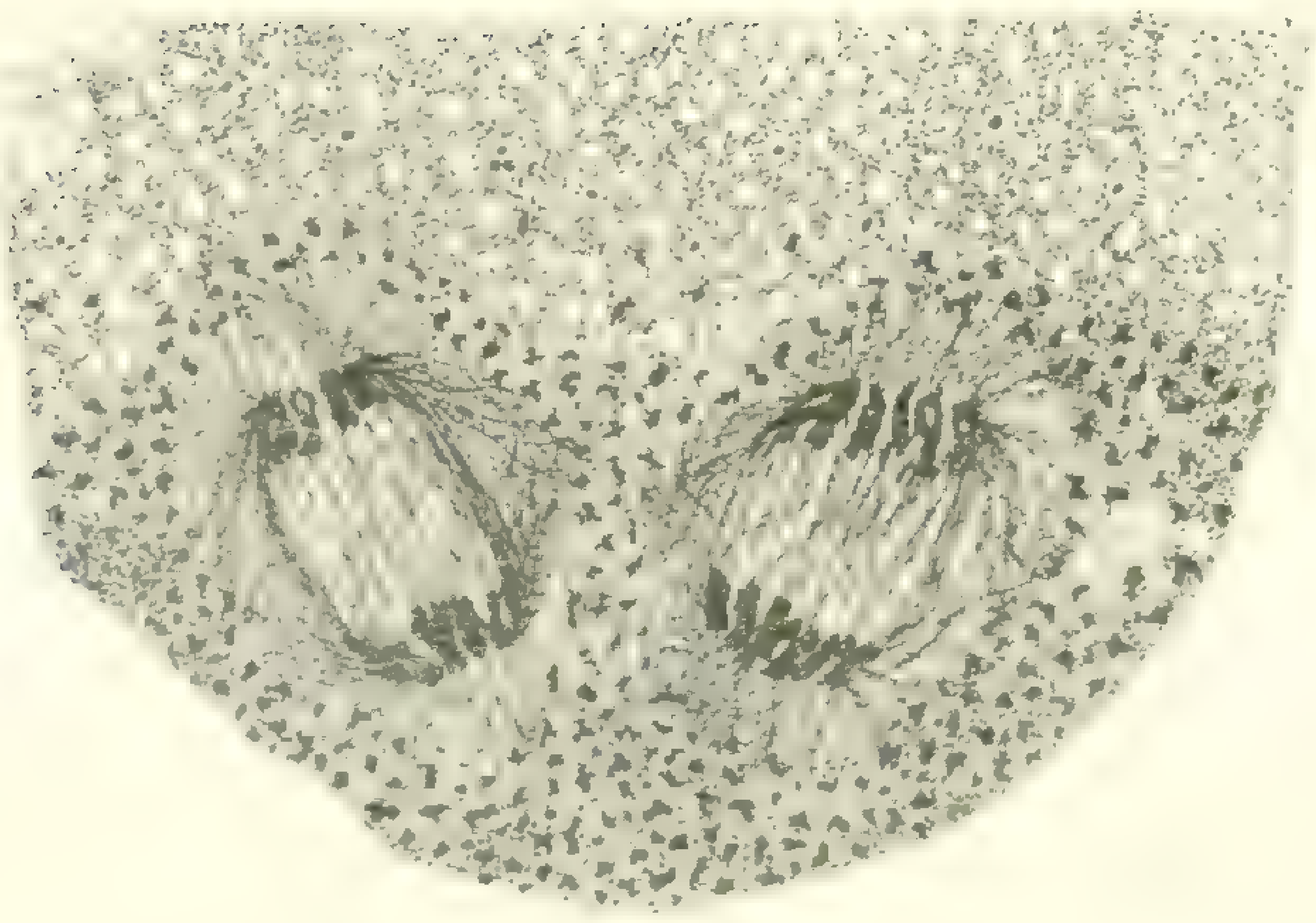
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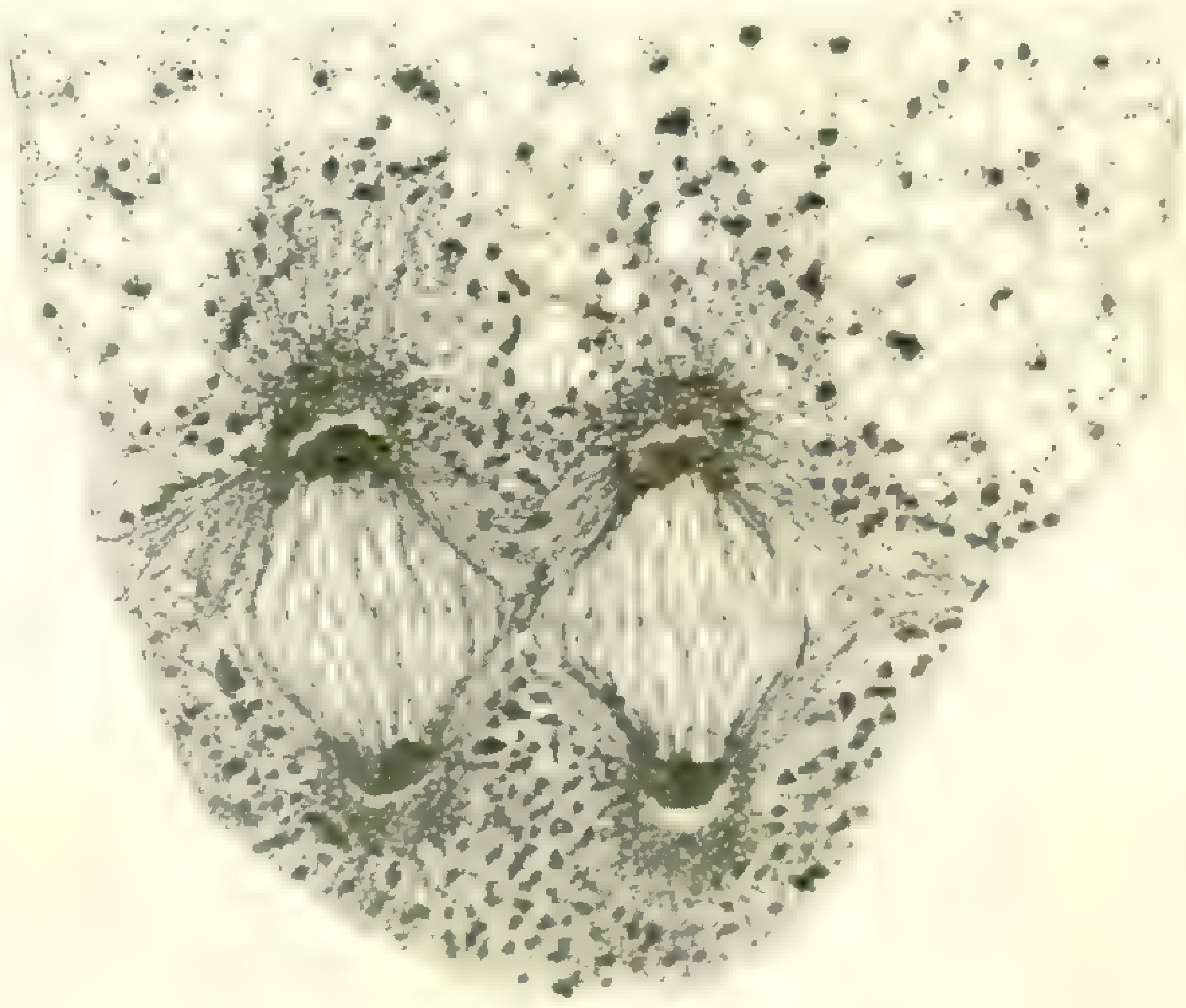
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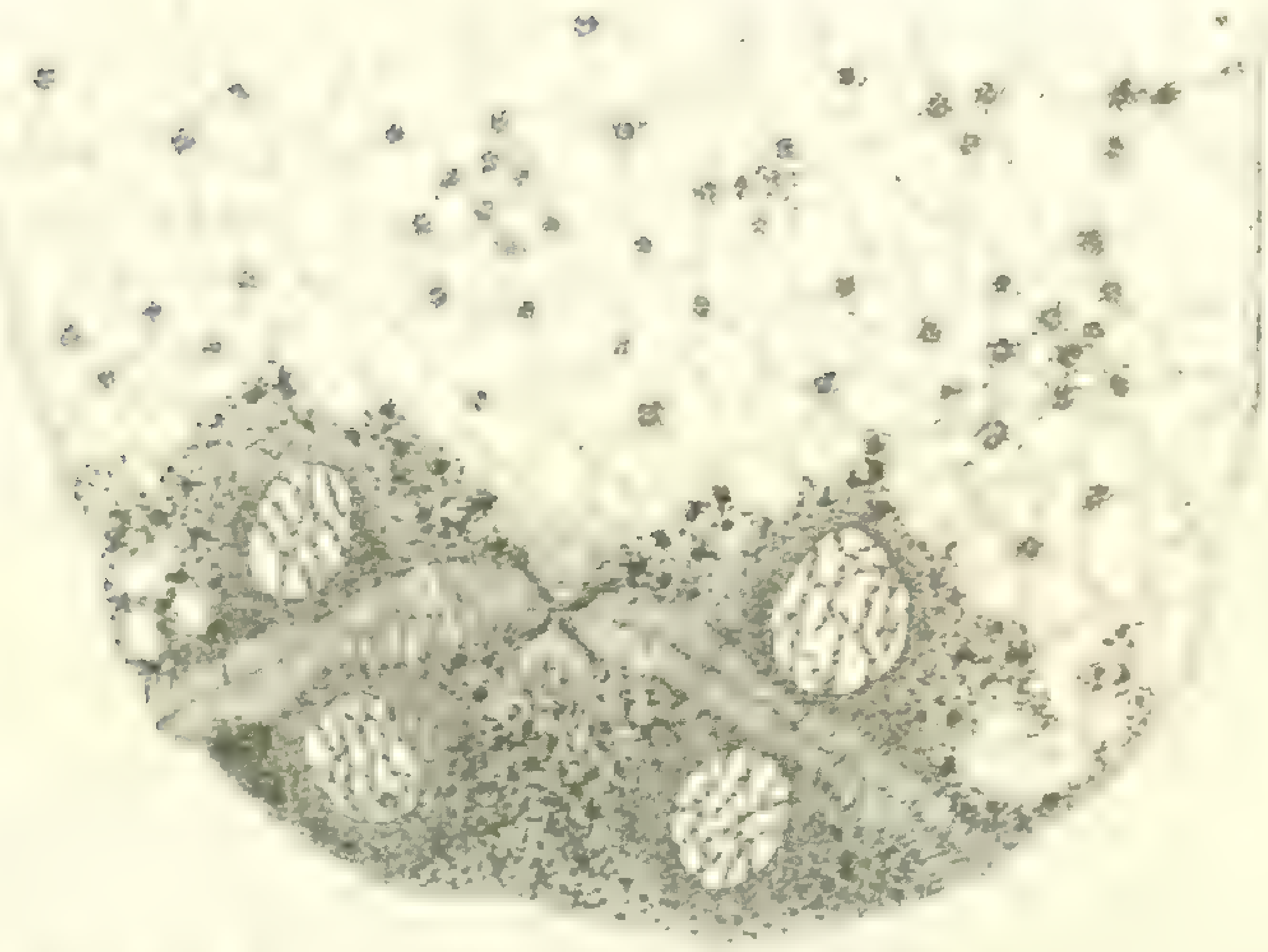
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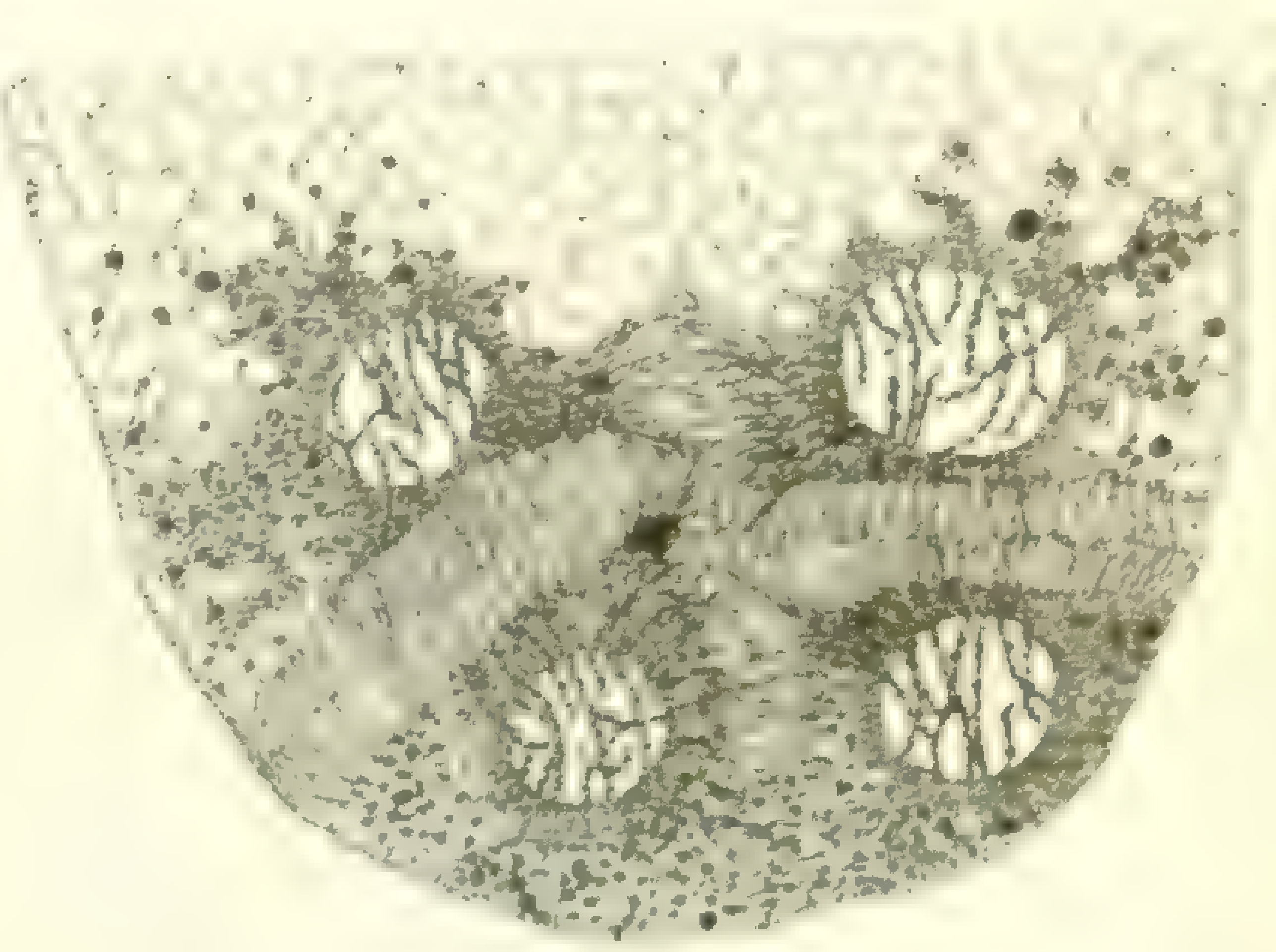
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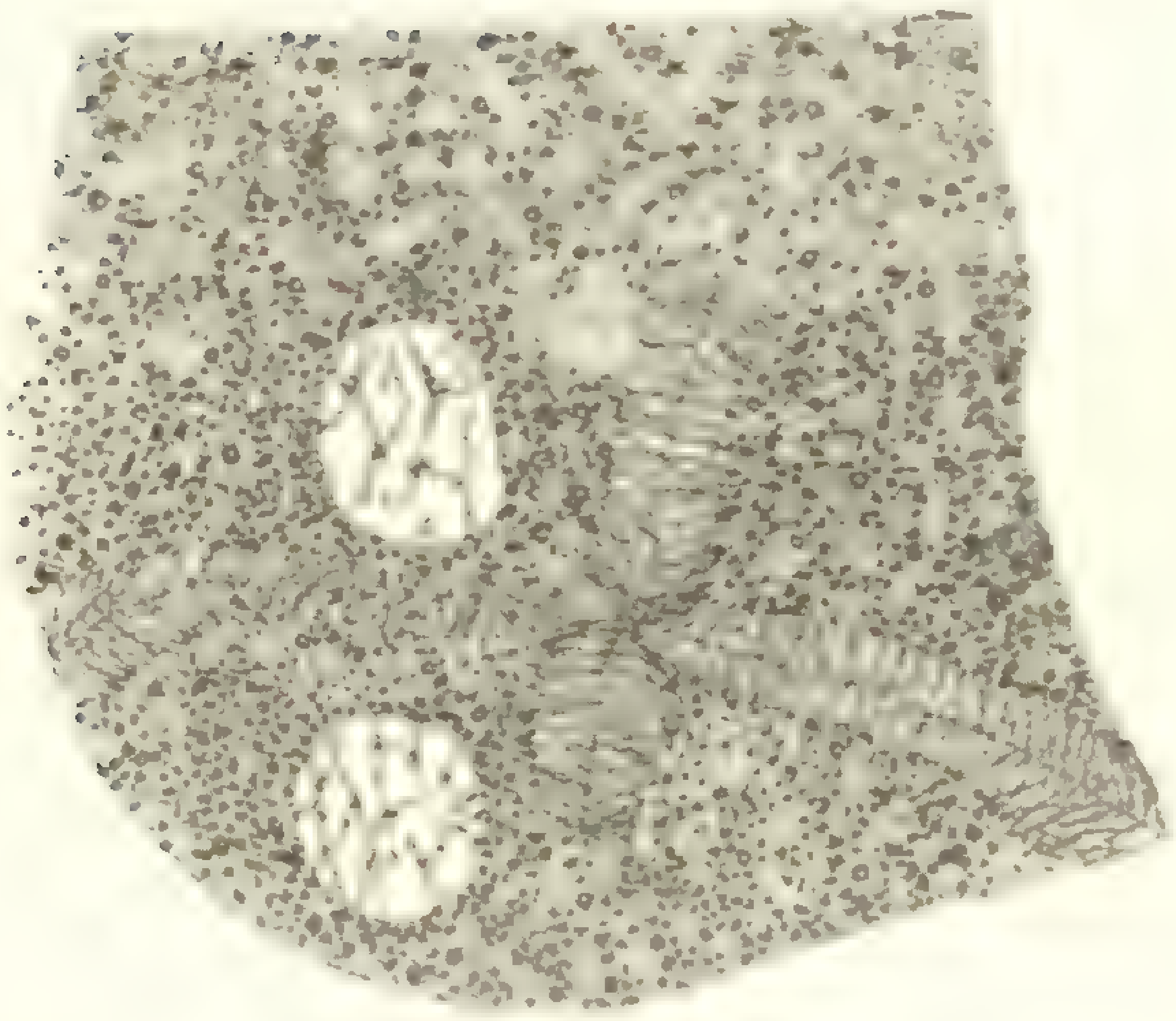
KILDAHL on PROEMBRYO



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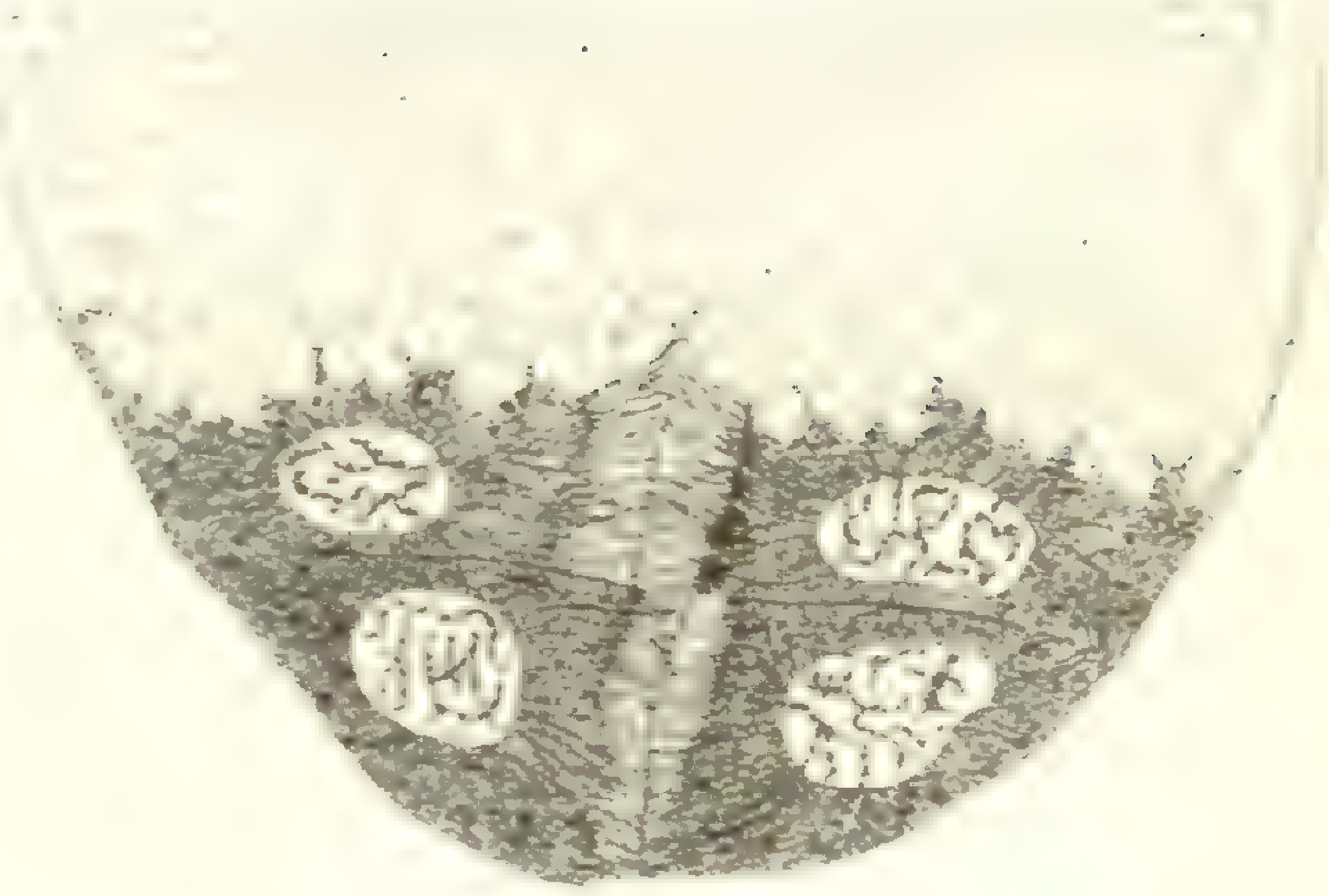

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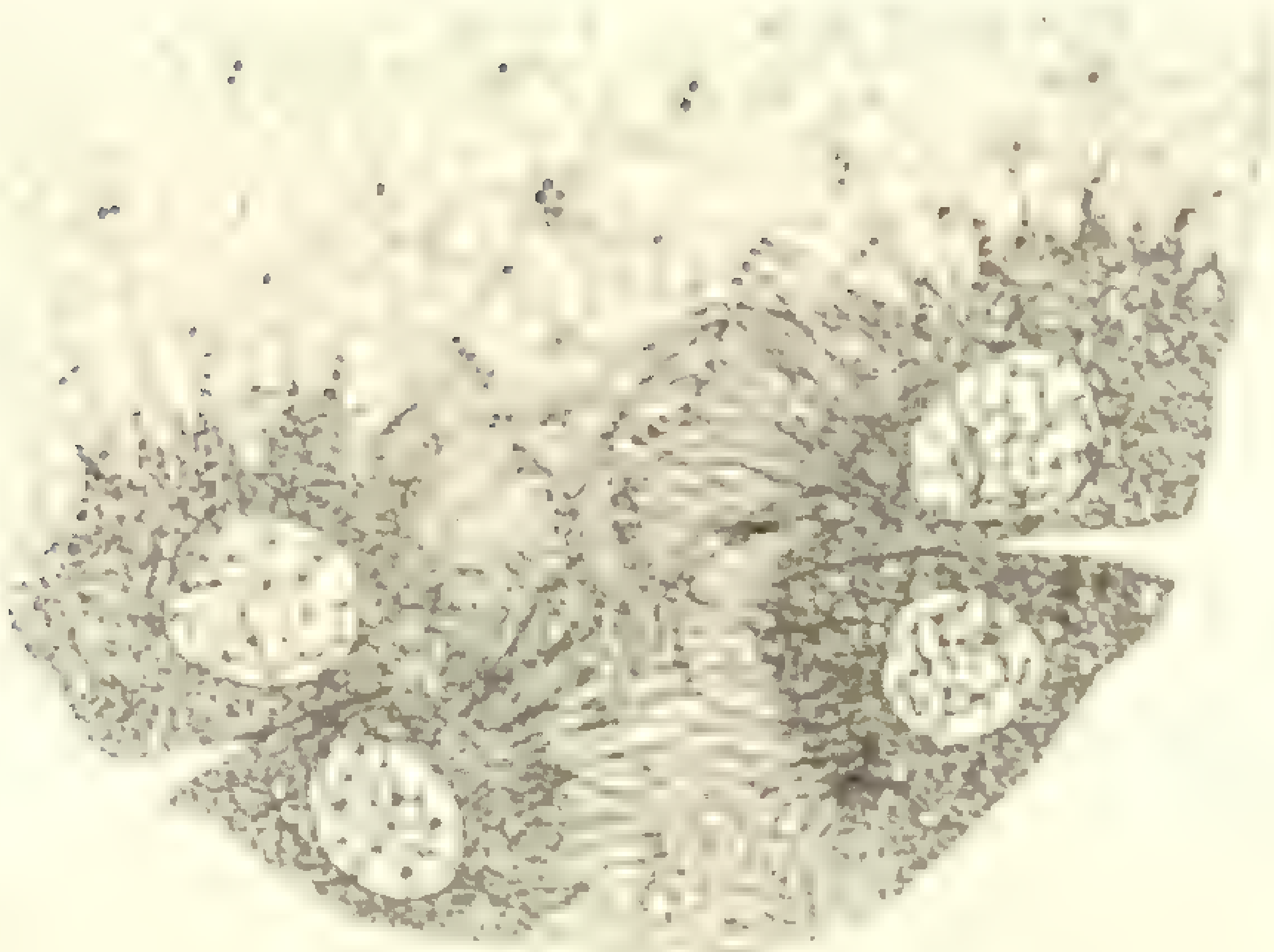

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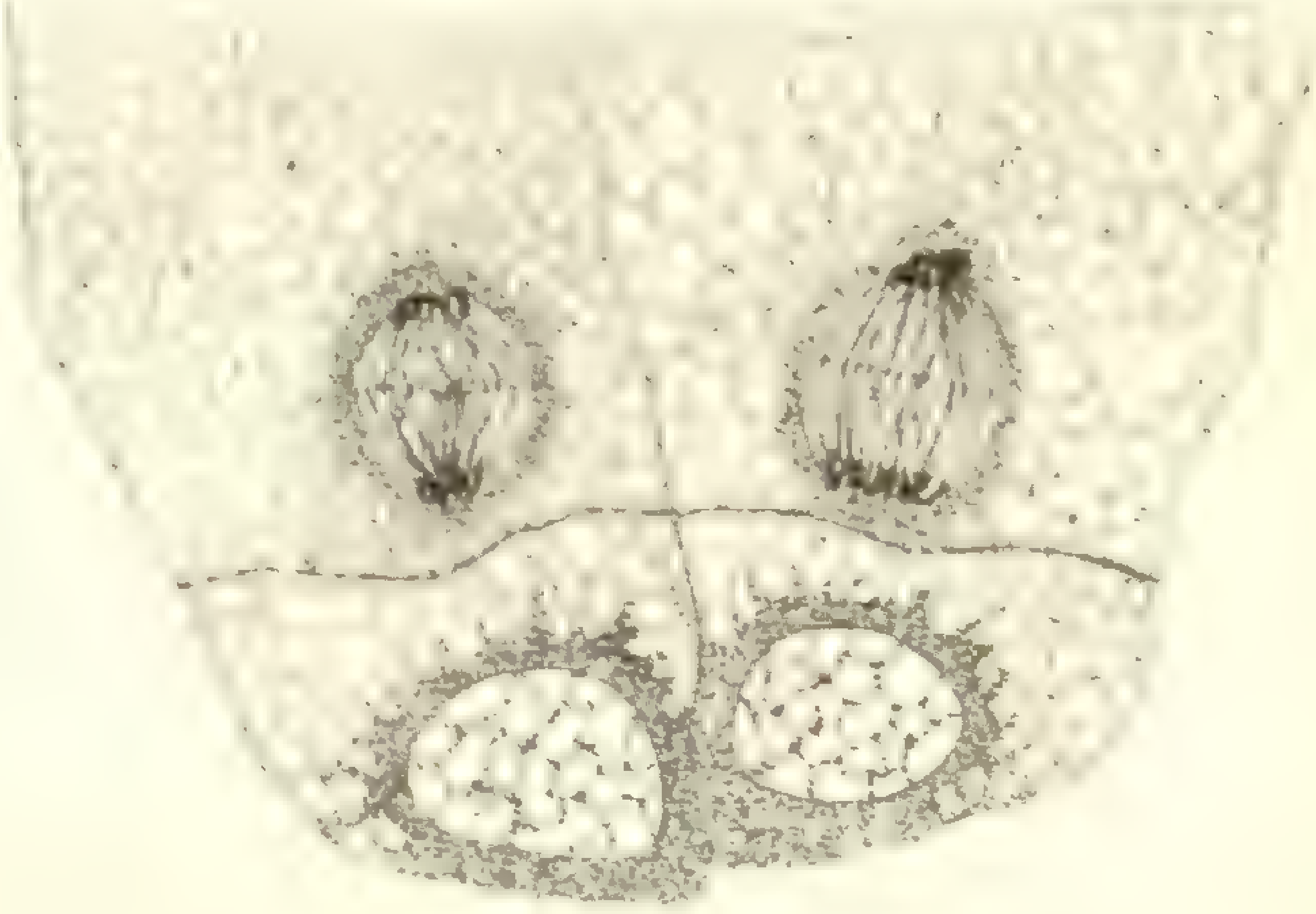

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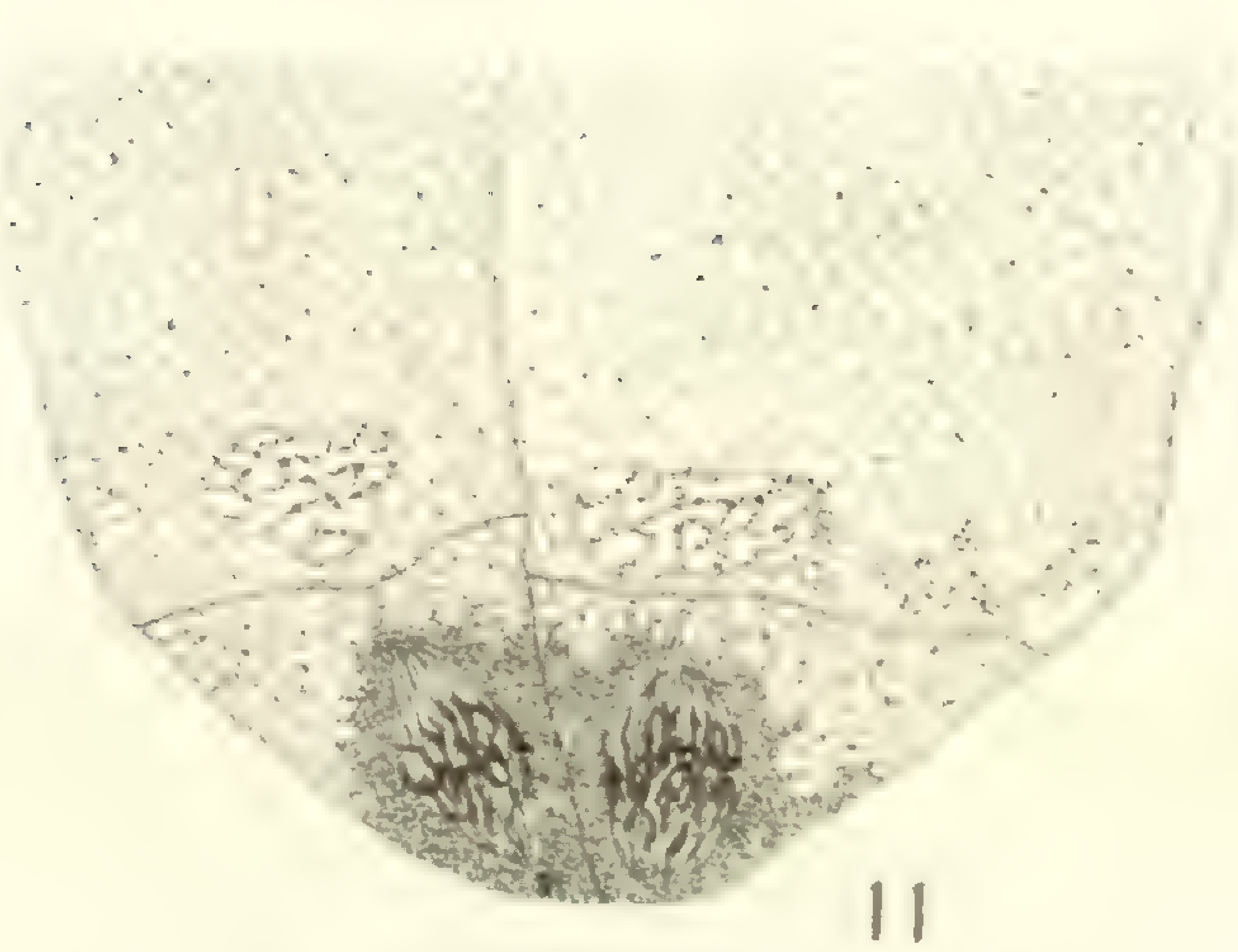

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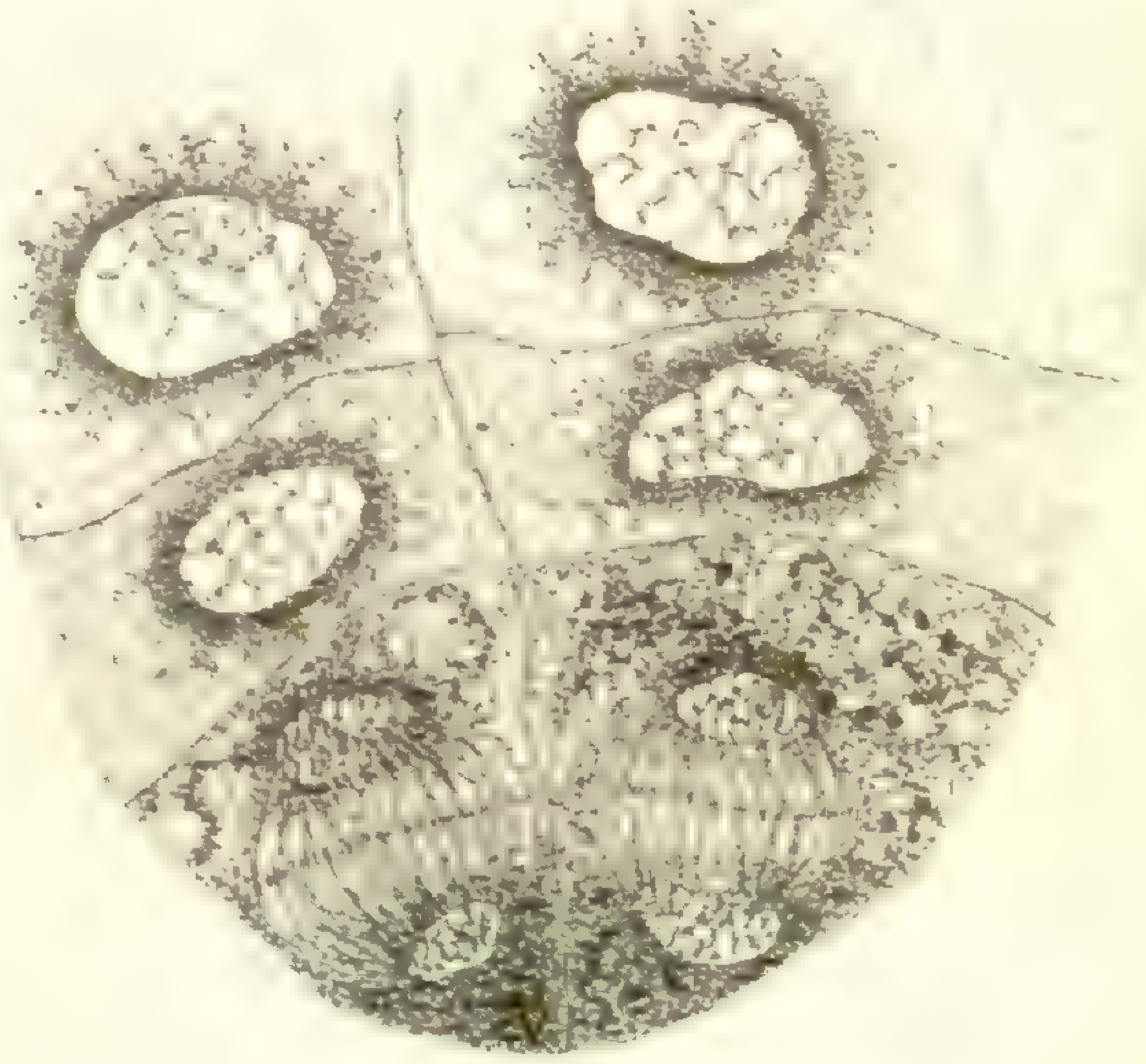

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N. Johanna Kildahl, Del.

KILDAHL on PROEMBRYO

PLATE IX

FIG. 7. Section showing the two walls more nearly in the same stage, but the cross wall a little in advance of the vertical. ×425.

FIG. 8. Section showing the vertical walls of each tier formed by the fibers from the nuclei of their respective tiers; the cross wall nearly complete. ×350.

FIG. 9. Same as *fig. 8;* the broad effect of the vertical wall caused by the section being cut a little to one side of the crossing of the two vertical walls. ×350.

FIG. 10. Second division. ×425.

FIG. 11. Second division. ×355.

FIG. 12. Third division. ×393.

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS

XIX[1]

JOHN DONNELL SMITH

Nissolia costaricensis Donn. Sm.—Foliola 5 glabra magna oblongo-vel ovato-elliptica obtuse curvilineo-acuminata basi acuta vel rotundata. Flores in pedunculo axillari brevissimo fasciculati vel rhachi evoluta racemosi. Calyx brevissime setaceo-denticulatus. Alae cum carina acute acuminatae. Legumen valde curvatum inter semina vix constrictum, ala maxima obtusa.

Suffruticosa, ramulis petiolisque minute setaceo-muriculatis ceterum glabris. Petiolus communis 7–11^{cm} longus, foliolis 5–8^{cm} longis 25–35^{mm} latis mucronulatis. Pedunculi nodiformes vel 4^{mm} longi et racemi pubescentes, his usque ad 5–8^{cm} longis, floribus 9^{mm} longis. Calyx pubescens turbinato-campanulatus parum obliquus 3^{mm} longus inter setas vix 0.5^{mm} longas truncatus. Vexillum extus pubescens 7^{mm} longum petalis reliquis paulo brevius. Ovarium pubescens plerumque 3-ovulatum, stylo angulo fere recto divergente. Leguminis stipes calyce altero tanto longior, corpus seminiferum canescens 11–22^{mm} longum 4^{mm} crassum, articulis 1–3 oblongis transverse subteretibus, mesocarpio intricato-fibroso, endocarpio araneoso, ala 24–28^{mm} longa 9–11^{mm} lata cum articulis arcuata.

In planitiis ad Surubres, Prov. Alajuela, Costa Rica, alt. 200^{m}, Jan. 1892, *P. Biolley* (n. 7088).—In fundo *La Verbena* dicto prope Alajuelita, Prov. San José, Costa Rica, alt. 1140^{m}, Dec. 1894, *H. Pittier* (n. 9664).

Machaerium (§ RETICULATA Benth.) **cobanense** Donn. Sm.—Stipulis bracteisque aculeatum. Foliola 13–19 elliptico-oblonga utrinque rotundata vel nunc apice nunc basi acutiuscula supra pube conspersa subtus sordide tomentulosa. Panicula longissima, floribus pedicellatis. Calyx braceolis vix bis longior breviter obtuseque tridentatus. Stamina aequaliter diadelpha.

In fruticetis reclinans, caulibus usque ad 10^{m} longis (cl. repertor in literis). Petiolus communis 9–15^{cm} longus, foliolis penninerviis reticulato-venosis mucronulatis, superioribus 4–5^{cm} longis 15–20^{mm} latis quam infima ovalia 3-plo longioribus, terminali maximo obovato-elliptico. Panicula sordide pilosa usque ad 3^{dm} longa, ramis saepe 2–3-nis erecto-patentibus, bracteis sicut stipulae induratis elongato-triangularibus 3–4^{mm} longis recurvis subpersistentibus, pedicellis 2–4^{mm} longis, bracteolis reniformi-cordatis 3.5^{mm} altis 5^{mm} latis, floribus 12^{mm} longis violaceis. Calycis pilosi tubus 5^{mm} longus, dentes inferiores oblongi 1.5–2^{mm} longi, superiores latissimi vix ulli. Vexillum extus cano-sericeum suborbiculatum emarginato-bilobum alis paulo carina multo longius. Stamina 6^{mm} longa ob vaginam utrinque fissam in phalanges 2 pentandras coalita. Ovarium villosum rectum longe stipitatum uniovulatum, disco cupuliformi, stylo incurvo. Legumen non suppetit.

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[1] Continued from BOT. GAZETTE 42:300. 1906.

Prope Cobán, Guatemala, alt. 1350^{m}, Aug. 1906, *von Tuerckheim* (n. II. 1401).

Machaerium (§ ACUTIFOLIA Benth.) **campylocarpum** Donn. Sm. —Inerme. Foliola 7–9 dissita lanceolata vel ovato-lanceolata acuta vel acuminata supra glabra subtus praeter costam glabrescentia. Racemi axillares breves arcte floriferi, floribus subsessilibus. Petala extus villosa. Stamina monadelpha. Legumen insigniter incurvum.

Petiolus communis 6–9^{cm} longus cum petiolulis pubescens, foliolis chartaceis concoloribus reticulato-penninerviis et venosis ad nervos venasque parce ad costam densius appresso-pilosis, lateralibus superioribus e basi obtusa lanceolatis 50^{mm} longis 15^{mm} latis, inferioribus ovato-lanceolatis acuminatis 35^{mm} longis, terminali basi acuto 65^{mm} longo. Racemi ferrugineo-pubescentes circiter 25^{mm} longi, bracteis bracteolisque semiorbicularibus 1.5^{mm} longis, floribus 8^{mm} longis. Calyx appresse ferrugineo-pilosus 3^{mm} longus vix denticulatus. Omnia petala dense longeque ferrugineo-villosa. Vexillum orbiculare 7^{mm} longum. Carinae petala angusta cum staminibus 6^{mm} longa. Ovarium pubescens uniovulatum. Leguminis glabrescentis breviter stipitati 5–6^{cm} longi corpus monospermum 9^{mm} latum, sutura superior ad semen abrupte inflexa, ala 35–40^{mm} longa 15–17^{mm} lata obtusa margine superiore arcuata inferiore recta.

In fundo *Jiménez* dicto ad Peñas Blancas, Rió Diquis, Comarca de Puntarenas, Costa Rica, alt. 600^{m}, Febr. 1898, *H. Pittier* (n. 12163).

Drepanocarpus (§ LINEATI Benth.) **salvadorensis** Donn. Sm.—Cano-pubescens vel-furfuraceus stipulis uncinatis aculeatus. Foliola 9–11 oblongo-obovata vel elliptica apice retusa basi acuta vel obtusa. Paniculae axillares binae et terminales, floribus pedicellatis. Petala subaequalia. Stamina aequaliter diadelpha cum carina valde incurva. Ovarium uniovulatum.

Stipulae indurato-spinescentes dilatatae 3–5^{mm} longae. Petioli communes 4–5^{cm} longi, foliolis plerumque 9 primum dense denique leviter pubescentibus coriaceis plerumque oblongo-obovatis 20–32^{mm} longis 11–15^{mm} latis insigniter retusis lineato-nervosis, nervis interdum anastomosantibus, margine nerviformi. Paniculae canescentes 6–11^{cm} longae, ramis singulis vel 2–3-nis, inferioribus

15–20^{mm} longis, pedicellis 2–3^{mm} longis, bracteolis suborbicularibus 2.5^{mm}-diametralibus persistentibus, floribus 12–14^{mm} longis. Calyx pubescens 7^{mm} longus, dentibus rotundatis 1^{mm} longis, 2 superioribus latioribus. Vexillum extus pubescens suborbiculare 10–11^{mm} longum 9^{mm} latum vix emarginatum alis aequilongum. Stamina carinam 9^{mm} longam quasi cucullatam aequantia, vagina ante anthesin utrinque usque ad basin fissa. Ovarium pubescens jam drepaniforme. Legumen ignotum.

Soyapango, Depart. San Salvador, Republ. del Salvador, alt. 750^{m}, Dec. 1906, ***Luís V. Velasco***, n. 9008 ex Pl. Guat. &c. quas ed. Donn. Sm.

Lonchocarpus minimiflorus Donn. Sm.—Foliola 7–11 lanceolato-elliptica acuminata basi acuta impunctata utrinque minute appresseque pubescentia. Racemi singuli densiflori, pedicellis per paria pedicello communi brevi insidentibus, floribus in genere minimis. Vexillum extus sericeum intus basi biappendiculatum. Alae et carina glabrae.

Arbor 8–10-metralis, ramulis lenticellatis. Petiolus communis 4–9^{cm} longus tetragonus pubescens. Petiolulus terminalis ceteris 3-plo longior medio articulatus. Foliola lateralia superiora 3–4^{cm} longa infimis ovalibus bis fere longiora, foliolum terminale obovato-lanceolatum 5–6^{cm} longum. Racemi tetragoni pubescentes pedunculo circiter 1^{cm} longo nonnunquam bifido adjecto 6–8^{cm} longi, pedicello communi 1.5^{mm} longo pedicellis propriis paulo longiore, bracteolis calyci approximatis ovalibus 1^{mm} longis persistentibus, floribus 5^{mm} longis. Calyx appresse aureo-pubescens vix dentatus 2^{mm} altus. Vexillum orbiculare 5^{mm} longum atque latum apice emarginatum dorso incanum. Alae et carina inter se aequilongae. Staminum tubus 3.5^{mm} longus, filamento vexillari omnino soluto. Ovarium cano-sericeum 5–6-ovulatum. Legumen non visum.—*L. parvifloro* Benth. et *L. atropurpureo* Benth. proximus.

Santa Bárbara, Depart. Sololá, Guatemala, alt. 450^{m}, Jan. 1894, *Heyde et Lux*, n. 6330 ex Pl. Guat. &c. quas ed. Donn. Sm.

Derris (§ EUDERRIS Benth.) **costaricensis** Donn. Sm.—Foliola 5–7 inter maxima obovato- vel oblongo-elliptica vel ovalia apice retusiusculo rotundata basi acuta vel obtusa punctata utrinque praesertim subtus molliter pubescentia transversim venosa. Pedicelli bini. Vexillum appendiculatum. Stamina monadelpha. Legumen cartilagineum velutinum lanceolato-ellipticum monospermum.

Ex ramulis ad apicem versus 6–8^{mm} crassis verisimiliter arborescens, partibus novellis luteo-fusco-velutinis. Petiolus communis 9–16^{cm} longus velutinus, petiolulo terminali 22^{mm} longo lateralibus 3-plo longiore. Foliola coriacea discoloria supra glabrescentia subtus aetate provectiore saltem in sicco minute foveolata, superiora 11–16^{cm} longa 6–8^{cm} lata, infima ovalia 6^{cm} longa 45^{mm}

lata, nervis luteo-fuscis, lateralibus utrinque 10–12 subrectis marginem attingentibus interdum anastomosantibus, venis transversis crebris subparallelis. Racemi axillares velutini 9–11^{cm} longi, pedicellis 8^{mm} longis, floribus 15^{mm} longis. Calyx velutinus 5.5^{mm} longus breviter setaceo-tridenticulatus. Vexillum orbiculare extus cano-sericeum basi sicut in Sectione *Paraderris* bicallosum. Alae glabrae. Carina extus sericea. Stamen vexillare ima basi tantum liberum, vagina 11^{mm} longa etiam post anthesin clausa. Ovarium pilosum uniovulatum stylo glabro 6^{mm} longo. Legumen luteo-fusco-velutinum 10–12^{cm} longum 4^{cm} latum vertice obtusum basi acutum, sutura superiore ala 1.5^{mm} lata marginata, semine coccineo reniformi 9^{mm} longo 18^{mm} lato.—Nomen vernaculare nempe *Siete Cueros* corticem exfoliantem vult indicare.—Genus adhuc tantum ex America Australi et Orbe Vetere cognitum.

Ad litora sinus *Salinas* dicti, Comarca de Puntarenas, Costa Rica, Jul. 1890, *Tonduz* (n. 2880).—In collibus silvestribus, Peninsula Nicoya, Costa Rica, Maj. 1900, *Tonduz* (n. 13993).

Derris (§ EUDERRIS Benth.) **peninsularis** Donn. Sm.—Glabra. Foliola 5–7 lanceolato-elliptica vel elliptica graciliter acuteque acuminata basi acuta punctulata subtus puberula crebre penninervia. Pedicelli bini pedicello communi insidentes. Vexillum appendiculatum. Stamina monadelpha. Ovarium 4–5-ovulatum. Legumen cartilagineum obliquum utrinque acuminatum, monospermum ovale, dispermum oblongum.

Ramuli verrucosi. Petiolus communis 8–11^{cm} longus, petiolulo terminali 24^{mm} longo ceteris 4-plo longiore. Foliola chartacea concoloria 6–10^{cm} longa 3–4^{cm} lata, nervis lateralibus utrinque 10–12 usque ad marginem simplicibus. Racemi axillares glabri 6–10^{cm} longi floribundi, pedicellis propriis medio bibracteolatis 2^{mm} longis pedicellum communem subaequantibus, floribus 11^{mm} longis. Calyx glabrescens 4^{mm} altus obsolete denticulatus. Vexillum lineis pubescentibus extus striatum basi bicallosum. Petala reliqua hinc illinc pubescentia. Stamina 8^{mm} longa, vexillari ima basi libero, vagina etiam post anthesin clausa. Ovarium pilosum. Legumen glabrum inaequilaterale 35^{mm} latum, monospermum 55–65^{mm} longum, dispermum 85^{mm} longum, sutura superiore ala 2^{mm} lata marginata, semine fusco reniformi 11^{mm} longo 21^{mm} lato.—Ab incolis *Chaperno* nuncupatur.

In silvis et ad vias, Peninsula Nicoya, Costa Rica, Maj. 1900, *Tonduz* (nn. 13961, 13966).

Derris (§ EUDERRIS Benth.) **nicoyensis** Donn. Sm.—Glabra. Foliola 5 rhomboideo-elliptica obtuse contracto-acuminata basi acuta impunctata subtus appresse cano-puberula penninervia. Pedicelli sparsi. Legumen cartilagineum ovale utrinque acuminatum monospermum.

Arbor, coma sphaeroidi (*Tonduz* in schedula). Petiolus communis glaber 7–12^{cm} longus, petiolulo terminali 24^{mm} longo lateralibus 4-plo longiore. Foliola coriacea supra glabra 55–90^{mm} longa 30–50^{mm} lata subcaudato-acuminata, nervis lateralibus utrinque 10–11 prope marginem arcuatis, venis grosse reticulatis. Racemi axillares, fructiferi solum cogniti 4–7^{cm} longi. Legumen glabrum aequilaterale circiter 65^{mm} longum 33^{mm} latum, sutura superiore ala 2^{mm} lata marginata, semine fusco reniformi 11^{mm} longo 18 ^{mm} lato.

In collibus silvestribus, Peninsula Nicoya, Costa Rica, Dec. 1899, *Tonduz* (n. 13547).

Inga (§ PSEUDINGA; Ser. *Vulpinae* Benth.) **Tonduzii** Donn. Sm. —Setuloso-hirsuta. Petioli alati, foliolis 2–3-jugis ellipticis vel ovato-ellipticis acuminatis basi obtusis. Pedunculi singuli vel bini spicae rhachin subaequantes. Corolla villosa calycem parce setuligerum bis superans. Legumen hirsutum planum marginibus incrassatum vix dilatatum.

Arbor, coma rotunda (*Tonduz* in schedula), ramulis petiolis pedunculis patenter denseque ferrugineo-setulosis. Stipulae deltoideae attenuato-acuminatae 10–12^{mm} longae 6–7^{mm} latae coriaceae striatae glandulosae extus hirsutae caducae. Petiolus inter foliolorum juga 2–4^{cm} longus 6–8^{mm} latus, infra jugum infimum 15–20^{mm} longus nudus, glandulis ellipsoideis, foliolis saepius trijugis coriaceis utrinque ad nervos dense inter nervos parcius hirsutis filiforme cuspidatis, supremis maximis 12–17^{cm} longis 6–9^{cm} latis par infimum 3–4-plo excedentibus. Pedunculi circiter 2^{cm} longi, spicis densifloris, bracteolis lineari-lanceolatis 7–10^{mm} longis extus hirsutis subpersistentibus. Calyx in lobos vel dentes acutos dirumpens praeter setulas sparsas glaber. Corolla pallide flavida 27^{mm} longa usque ad quintam partem superiorem acute lobata. Stamina rosea corollam bis superantia, tubo incluso. Ovarium glabrum. Legumen 17^{cm} longum 38^{mm} latum marginibus 4^{mm} crassum.—*I. insignem* Kunth et *I. Pittieri* Micheli revocans ab utraque tamen legumine sectionis distinctissima.

Las Vueltas, Tucurrique, Costa Rica, alt. 635^{m}, Dec. 1898, *Adolfo Tonduz* (n. 12928).

Faramea (§ HYPOCHASMA Muell. Arg.) **suerrensis** Donn. Sm.—(*F. trinervia* K. Schum. et Donn. Sm., var. *suerrensis* Donn. Sm.)—Folia obovato-vel oblongo-elliptica vel lanceolata in caudam gracilem acuminata basi acuta trinervia. Cyma foliaceo-bibracteata. Pedicelli floribus breviores. Calycis tubus turbinatus, limbus mucronulis denticulatus disco brevior. Alabastrum loborum corollae subglobosum. Filamenta longiuscula. Fructus transversim ellipsoideus.

Frutex 3–4^{m} altus ramosus. Folia crasso-pergamenea diaphana nitida concoloria 16–22^{cm} longa 4–7^{cm} lata in caudam 14–20^{mm} longam desinentia, costa utrinque prominente, nervo conspicuo a basi utrinque prodeunte apicem attingente a margine 5–8$^{\text{mm}}$ distante, nervis lateralibus primariis angulo fere recto a costa divergentibus utrinque 14–16, petiolis 8–12$^{\text{mm}}$ longis, stipulis persistentibus vaginantibus 7–9$^{\text{mm}}$ longis muticis. Pedunculus 4–5$^{\text{cm}}$ longus apice bracteis lanceolatis 4$^{\text{cm}}$ longis caducis instructus, cyma foliis breviore densiflora repetitus trichotoma, pedicellis 4–6$^{\text{mm}}$ longis. Calycis tubus 1$^{\text{mm}}$ longus limbo intus glanduloso bis longior, denticulis minutis. Corolla intense cyanea 9$^{\text{mm}}$ longa tertia parte lobata ore constricta. Stamina corollae ad basin versus inserta, filamentis 1.5$^{\text{mm}}$ longis, antheris inclusis. Discus cylindricus 1$^{\text{mm}}$ longus. Fructus cyaneus transversim 15$^{\text{mm}}$ longus 11$^{\text{mm}}$ crassus, semine conformi subtus usque ad medium transversim bipartito.

In silvis profundis udisque ad fundum *Suerre* dictum, Llanuras de Santa Clara, Costa Rica, alt. 300$^{\text{m}}$, Febr. 1896, *J. Donnell Smith*, n. 6589 ex Pl. Guat. &c. quas ed. Donn. Sm.—In silvis prope confluentiam fluminum Puerto Viejo et Sarapiquí, Llanuras de Tortugero, Costa Rica, alt. 120$^{\text{m}}$, Febr. 1893, *P. Biolley* (n. 7394).

Faramea (§ HYPOCHASMA Muell. Arg.) **eurycarpa** Donn. Sm.—Folia obovato-vel elliptico-oblonga caudato-acuminata basi acuta subtus flavo-virentia, nervis lateralibus validioribus remotis prope marginem arcuatim connexis. Cyma folia subaequans laxiflora, pedicellis gracillimis. Calycis lobi inaequales apice recurvati. Fructus transversim oblongo-ellipsoideus.

Arbuscula, ramulis flavo-virentibus. Folia tenuiter chartacea diaphana discoloria 11–15$^{\text{cm}}$ longa 4–5$^{\text{cm}}$ lata in caudam 10–12$^{\text{mm}}$ longam contracta, nervis lateralibus patentissimis utrinque 8–10, petiolis 4–5$^{\text{mm}}$ longis, stipulis cito caducis ignotis. Pedunculus 4–6$^{\text{cm}}$ longus, bracteis ovalibus 4$^{\text{mm}}$ longis aristulatis, cyma subcorymbiformi quater quinquiesve trichotoma, pedicellis 10–13$^{\text{mm}}$ longis. Calycis tubus campanularis 2$^{\text{mm}}$ longus limbum atque discum aequans, lobi oblongo-ovati accrescentes, duo oppositi 3–6$^{\text{mm}}$ longi ceteris 2–3-plo majores. Corolla cyanea 10–11$^{\text{mm}}$ longa, loborum alabastro ovoideo 3.5$^{\text{mm}}$ longo. Stamina medio tubo corollae inserta, antheris subsessilibus 5$^{\text{mm}}$ longis inclusis. Discus truncato-conicus. Fructus transversim 12$^{\text{mm}}$ longus 6$^{\text{mm}}$ crassus, semine coeruleo basi transversim et profunde bipartito.

In silvis prope Las Vueltas, Tucurrique, Costa Rica, alt. 650–700$^{\text{m}}$, Dec. 1898, *A. Tonduz* (n. 12880).

Themistoclesia pterocarpa Donn. Sm.—Folia obovata apice rotundata basi attenuata obscure quintuplinervia. Flores solitarii. Calyx campanulatus pentapterus corolla 5-plo fere superatus. Antherae rimis linearibus dehiscentes, filamentis glabris. Fructus globosus alatus.

Fruticulus epiphyticus ramosus dense foliosus, ramulis novellis et petiolis pubescentibus. Folia plerumque 2^{cm} longa 1^{cm} lata coriacea praeter costam supra puberulam glabra, margine integro revoluto, nervis venisque praesertim subtus subimmersis, petiolis canaliculatis 1^{mm} longis. Pedunculi singuli tetragoni basi squamosi 6–7^{mm} longi et flores glabri. Calyx 4^{mm} longi, tubo quam limbus bis longiore. Corolla tubulosa 18–19^{mm} longa teres, lobis oblongo-ovatis 3.5^{mm} longis intus pubescentibus. Stamina tubum corollinum aequantia, filamentis aequalibus complanatis 4^{mm} longis, loculis granulatis 3.5^{mm} longis antice brevissime calcaratis, tubulis 10^{mm} longis tertia parte rimosis. Stylus corollam paulo superans. Fructus 6^{mm}-diametralis.—Calycis tubus *Anthopterum* simulat. Inflorescentia atque corolla necnon calycis limbus cum *Themistoclesia* melius congruunt.

In summo monte *Carizia* dicto, Costa Rica, alt. 2000^{m}, Sept. 1900, *H. Pittier* (n. 14031).

Centropogon (§ SIPHOCAMPYLOIDES Benth. et Hook.) **porphyrodontus** Donn. Sm.—Folia subcoriacea nitida lanceolato-ovata sensim tenuiterque elongata basi vix ac ne vix cordata calloso-denticulata. Pedunculi axillares. Calycis tubus poculiformis supra ovarium productus basi intrusus segmenta linearia aequans. Corolla anguste tubulosa recta. Staminum tubus glaber.

Suffrutex. Folia 7–13^{cm} longa 35–70^{mm} lata acutissima basi truncata vel retusa subtus pallidiora, denticulis salientibus 0.5^{mm} longis et margine revoluto purpureis, nervis subtus et petiolo 15–20^{mm} longo roseolis subtiliter puberulis. Pedunculi 6–9^{cm} longi sub flore deflexo torti. Calyx nitidus 14^{mm} longus, tubo bis longiore quam latiore, segmentis liberis integris acutis. Corolla glabra in sicco rosea 42–45^{mm} longa usque ad quintam partem lobata. Antherae dorso parce pilosae, minores vertice penicellatae. Bacca globoso-ovalis, 9^{mm} longa 7^{mm} lata.

Valle de Los Arcángeles, Prov. San José, Costa Rica, alt. 1900^{m}, Dec. 1898, *H. Pittier*, n. 7349 ex Pl. Guat. &c. quas ed. Donn. Sm.(n. 12307 herb. nat. Cost.).—Sub *Siphocampylo Costaricae* Vatke olim distributus.

Centropogon (§ SIPHOCAMPYLOIDES Benth. et Hook.) **nematosepalus** Donn. Sm.—Undique paleaceo-pubescens. Folia membranacea supra sparsim subtus densius pubescentia lanceolato-ovata sensim elongata basi cordata setulis excurrentibus denticulata. Pedunculi axillares. Calycis tubus obconicus segmentis filiformibus denticulatis bis superatus. Corolla incurva sursum sensim paulo ampliata. Staminum tubus cum antheris hirsutus.

Suffrutex scandens, partibus novellis canescentibus. Folia subtus pallida 75–100^{mm} longa 35–45^{mm} lata, denticulis minutis inaequalibus ciliolatis, nervis venisque subtus patenter pubescentibus, petiolis 35–45^{mm} longis. Pedunculi foliis breviores, floribus pubescentibus 46–50^{mm} longis. Calycis segmenta tenuissima 9^{mm} longa denticulis subulatis utrinque 3–4 munita. Corolla siccitate purpurea leviter incurva 42–45^{mm} longa, lobis 11^{mm} longis. Antherae exsertae, minores vertice penicellatae. Bacca ignota.—Speciei praecedenti foliorum circumscriptione similis eorum indumento et margine necnon florum indole satis differt.

Cuesta de los Borucas, Comarca de Puntarenas, Costa Rica, alt. 2300^{m}, Jan. 1897, *H. Pittier* (n. 10533).

CENTROPOGON NEMATOSEPALUS Donn. Sm., var. **palmanus** Donn. Sm.—Folia acuminato-ovata basi leviter cordata. Pedunculi foliis longiores usque ad 6–8^{cm} longi. Calycis segmenta integra tubum aequantia. Antherae dorso sicut staminum tubus glabrae. Bacca glabra globoso-ovalis.

La Palma, Prov. San José, Costa Rica, alt. 1500^{m}, Jul. 1888, *H. Pittier* (n. 271).

Ardisia (§ PICKERINGIA Mez.) **meiantha** Donn. Sm.—Folia parva lanceolato-elliptica utrinque acuta integra coriacea utrinsecus punctulata et eminenter minuteque reticulata. Flores bipinnatim paniculati in genere minimi 5–6-meri. Corollae lobi patentes staminibus breviores. Filamenta antheris quincuplex longiora.

Folia 40–70^{mm} longa 15–25^{mm} lata a medio utrinque fere consimiliter angustata subtus pallidiora, petiolis canaliculatis 5–7^{mm} longis. Panicula terminalis breviter pedunculata densiflora minutissime furfuracea 35–50^{mm} alta, ramis primariis racemose florigeris, infimis 10–15^{mm} longis, bracteis oblongo-ovatis 7^{mm} longis, pedicellis 2–3^{mm} longis in calycem basi incrassatum ampliatis, bracteolis ovatis 2^{mm} longis sicut bracteae rubro-punctatis et caducis. Flores plerumque 6-meri genitalibus porrectis computatis vix 3.5^{mm} longi. Sepala concava ovalia 1^{mm} longa marginibus minutissime ciliolata. Corolla 2^{mm} longa usque ad duas partes fere lobata, lobis imbricatis breviter oblongis obtusis uti sepala punctis et lineis rubro-notatis. Filamenta libera 2.5^{mm} longa, antheris acuminato-cordatis 0.5^{mm} longis medio affixis birimosis. Ovarium cum staminibus immaculatum ovoideum stylo subulato adjecto 3^{mm} longum 6–8-ovulatum. Fructus ignotus.

Prope Cartago, Costa Rica, alt. 1500^{m}, Apr. 1906, *William R. Maxon* (n. 44).—Typus in herb. Horti Botanici Noveboracensis servatur.

Rauwolfia stenophylla Donn. Sm.—Verticilli approximati tetraphylli. Folia lineari-lanceolata acuta in petiolum attenuata in quoque verticillo valde inaequalia crebre penninervia opaca. Cyma pseudoterminalis corymbiformis foliis bis terve superata dichotoma floribunda. Corollae tubus calyce 3-plo longior lobos proprios aequans infra medium staminiferus.

Glabra. Internodia ad apicem versus ramulorum 8–20^{mm} longa. Folia chartacea 9–17^{cm} longa 12–25^{mm} lata, cujusque verticilli folium maximum minimo bis longius, nervis lateralibus utrinque 30–35 prope marginem arcuatis, venis subobsoletis, petiolis canaliculatis 7–18^{mm} longis. Pedunculi alterni foliis nascentibus subopposti, inferiores 25^{mm} longi, ramis cymulisque dichotomis, pedicellis 2–6^{mm} longis, bracteolis ovatis vix 0.5^{mm} longis. Calyx 1.5^{mm} longus, lobis ovatis obtusis. Corolla 9–10^{mm} longa extus puberula ore cano-pilosa intus pubescens. Ovaria sejuncta disco cupuliformi cincta circiter 4-ovulata. Fructus deest.—*R. longifoliae* A. DC. ex characteribus proxima.

Republica del Salvador, loco natali haud accuratius indicato, ann. 1905, *Cárlos Rênson* (n. 289). Typum in herb. Musei Nationalis vidi.

Gonolobus (§ Monostemma K. Schum.) **Tuerckheimii** Donn. Sm.—Fusco-pilosus. Folia ovato-lanceolata coriacea discoloria costa cum petiolo villosa margine pilosa ceterum glabrescentia. Corymbi pedunculati simplices petiolo longiores. Corolla rotata reflexa marmorata, lobis orbicularibus. Corona ex lobulis 5 reflexis constans tubo stamineo elongato 3-plo superata. Stigma obtuse angulatum.

Frutex volubilis, caulibus retrorsum pilosis. Folia subtus saltem siccitate flavicantia, juniora subtus fusco-reticulata, provectiora 50–62^{mm} longa 22–26^{mm} lata apice acuta basi rotunda, nervis venisque subimmersis, petiolo 14–17^{mm} longo. Corymbi pilosi pedunculo 5^{mm} longo computato 20–26^{mm} longi 5–9-flori, pedicellis 8–15^{mm} longis, floribus 15–16^{mm}-diametralibus. Calyx extus patenter pilosus intus 5-glandulosus, segmentis ovato-lanceolatis acutis 6^{mm} longis. Corolla aurantiacea badio-reticulata extus puberula intus nuda, tubo 3^{mm} longo, lobis 6^{mm} longis. Coronae simplicis lobuli semiorbiculares. Tubus stamineus columnaris 1.5^{mm} longus. Pollinia clavata subpendula. Ovaria glabra, stigmate angulis haud producto 2.5^{mm} lato, centro depresso. Follicula non vidi.—Secundum characterum subordinationem Schumannianam prope *G. rhamnifolium* Griseb. locandus.

Cobán, Depart. Alta Verapaz, Guatemala, alt. 1320^{m}, Jul. 1906, *A. von Tuerckheim* (n. II. 1301).

Sanchezia Sprucei Lindau, var. **salvadorensis** Donn. Sm.—Arbuscula (cl. *Velasco* in scheda), ramulis obtuse tetragonis et foliis glabris. Cujusque paris folium alterum altero bis majus. Spicae in paniculam 14–16^{cm} longam dispositae internodiis nudis interruptae. Calycis segmenta cum bracteis bracteolisque glabra, 3 linearia, reliqua latiora deorsum angustata. Corolla usque ad 56^{mm} longa, lobis 5^{mm} longis atque latis. Antherae 6^{mm} longae. Stylus stigmate 5^{mm}

longo computato 65^{mm} longus.—Cum diagnosi exempli typici peruviani ceterum satis bene quadrant exempla salvadorensia.

In hortis ad oppidum San Salvador, Republ. del Salvador, alt. 700^{m}, Dec. 1906, *Luis V. Velasco*, n. 8985 ex Pl. Guat. &c. quas ed. Donn. Sm.

SAHAGUNIA UROPHYLLA Donn. Sm. in BOT. GAZ. **40**:11. 1905.—Descriptioni adde charactera emendata e specimine infra citato sumpta:—Folia tactu asperula. Capitula feminina solitaria et breviter pedunculata vel 2–4 in racemum $3–9^{cm}$ longum dissita subsessilia, perianthiis fructiferis 2–8 primum in massam carnosam velutinam concretis denique solutis.

Specimen n. 112 enumeratum a *Cárlos Rênson* in Republica *El Salvador* ann. 1905 lectum in herb. Musei Nationalis vidi.

BALTIMORE, MARYLAND

MICROCYCAS CALOCOMA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCVII

Otis W. Caldwell

(WITH PLATES X–XIII AND FOURTEEN FIGURES)

In a recent number of the Botanical Gazette (1) there appeared a brief taxonomic account of this plant. It was described originally by Miquel, from fragmentary material, as *Zamia calocoma* (2), although on account of its resemblance to a small *Cycas revoluta* he made for it the section Microcycas under Zamia. Later DeCandolle (3) added to Miquel's description and raised the section to generic rank. The previous paper (1) added to the knowledge of the taxonomic features of the species; while the present paper deals with the field studies and the morphology.

FIELD OBSERVATIONS

The region in which this study was made is in the Sierras of western Cuba, beginning with the mountains northwest of San Diego de los Baños, running through the Santa Catalina region, and ending to the westward with the mountain known locally as Cuchillo de Pinar, near San Andrace. Within this area Microcycas was found in four places, in three of which the plants were few and distinctly local. In the other (Cuchillo de Pinar) the plants were found one, two, or a half-dozen together at infrequent intervals for a distance of one and a half to two miles along the mountain. It is highly probable that sufficient search would result in the discovery of other groups in other mountains. The native Cuban mountaineers, to some of whom the plant is known as "palma corcho," reported that they had heard of the plant elsewhere, though they said it is extremely rare. The folk-lore of the region says that the roots of the "palma corcho" are good for use as rat poison, hence the desirability of a knowledge of its location, and the probability that there would be knowledge of any large groups of individuals should they exist.

The specimens observed were not confined to any particular exposure; the one shown in *fig. 3* is facing south; those in *figs. 1, 2,* and *4* are facing north; while those in *figs. 5* and *6* face west. In so far as could be determined, the plants are closely limited in elevation, the level showing them to be at essentially the same elevation though they vary greatly in their distances from the tops of the mountains upon which they grow. They were found growing on limestone, in places almost devoid of soil (*fig. 2*), in rocky soil (*fig. 3*), and in clay (*figs. 1, 4–6, 9*).

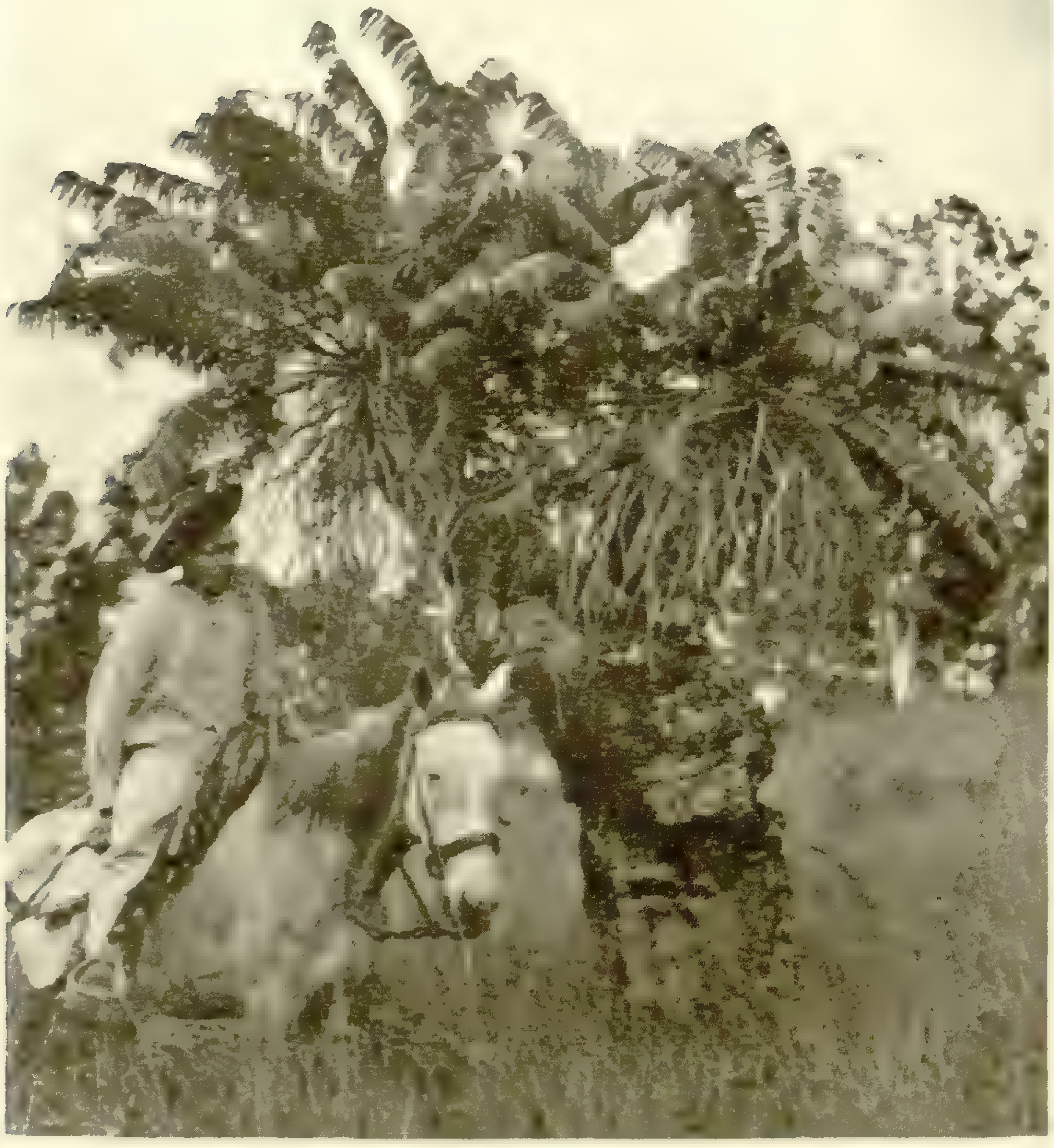

FIG. 1.—A plant 2^{m} in circumference at 1^{m} above ground; no other plants in this vicinity.

The roots show considerable ability to adjust themselves. In clay they sink deep into the soil, the stem and root system, in the case of younger plants, suggesting the geophilous habit of some of the Zamias. The plant shown in *fig. 9* was imbedded to within 3.75^{cm} of the top of the stem. This plant is 9.5^{cm} in diameter and is doubtless a good many years old, though relatively young. The geophilous habit is relatively temporary. As the plant becomes older its stem elongates, and at one period in this advance (*fig. 7*) the whole plant bears a marked resemblance to *Cycas revoluta*. The continued elongation of the stem results, at least in the case of those specimens that grow surrounded by taller plants of other species, in producing stems several meters in height (*figs. 2, 3, 4, 6*), the specimen at the right in *fig. 4* (showing neither base nor crown) being 9.5^{m} in length. The plants shown in *figs. 1* and *3* are doubtless the oldest plants observed. Both of these grow in the open and it seems not unlikely that they were once much taller than now, that they were injured by winds or otherwise, and that the branches now bearing leaves originated from dormant buds relatively late in the history of these individual plants. Evidence favoring such an interpretation is found in the facts that the terminal bud region of both these plants, and all similar ones observed, is injured and partially decayed; that the central starchy pith region of Microcycas is extremely brittle and would be easily broken if exposed to very heavy winds; and that many cases were observed of new branches arising from the surface of the plant body. One case was observed in which the young branch formed roots which penetrated the main body of the parent plant. Specimens of younger plants were found in the open, in which there was a single terminal crown of leaves, but none nearly so old as those shown in *figs. 1* and *3*. It may be that, if undisturbed, these would develop stems as old and thick and not attain greater height; but this does not seem probable.

The stem may be straight and unbranched (*figs. 2, 8*), or it may branch in a number of ways. In *fig. 4* is shown a group of four plants which arise from the stump of an older one. The decayed remains of the old stump, though not evident in the photograph, were observed, and showed clearly that the branches arose from the old stump below the surface of the ground. Other illustrations of branching are shown in *figs. 1, 3, 4, 6*.

Upon the surface of the stem of all younger plants, as well as upon

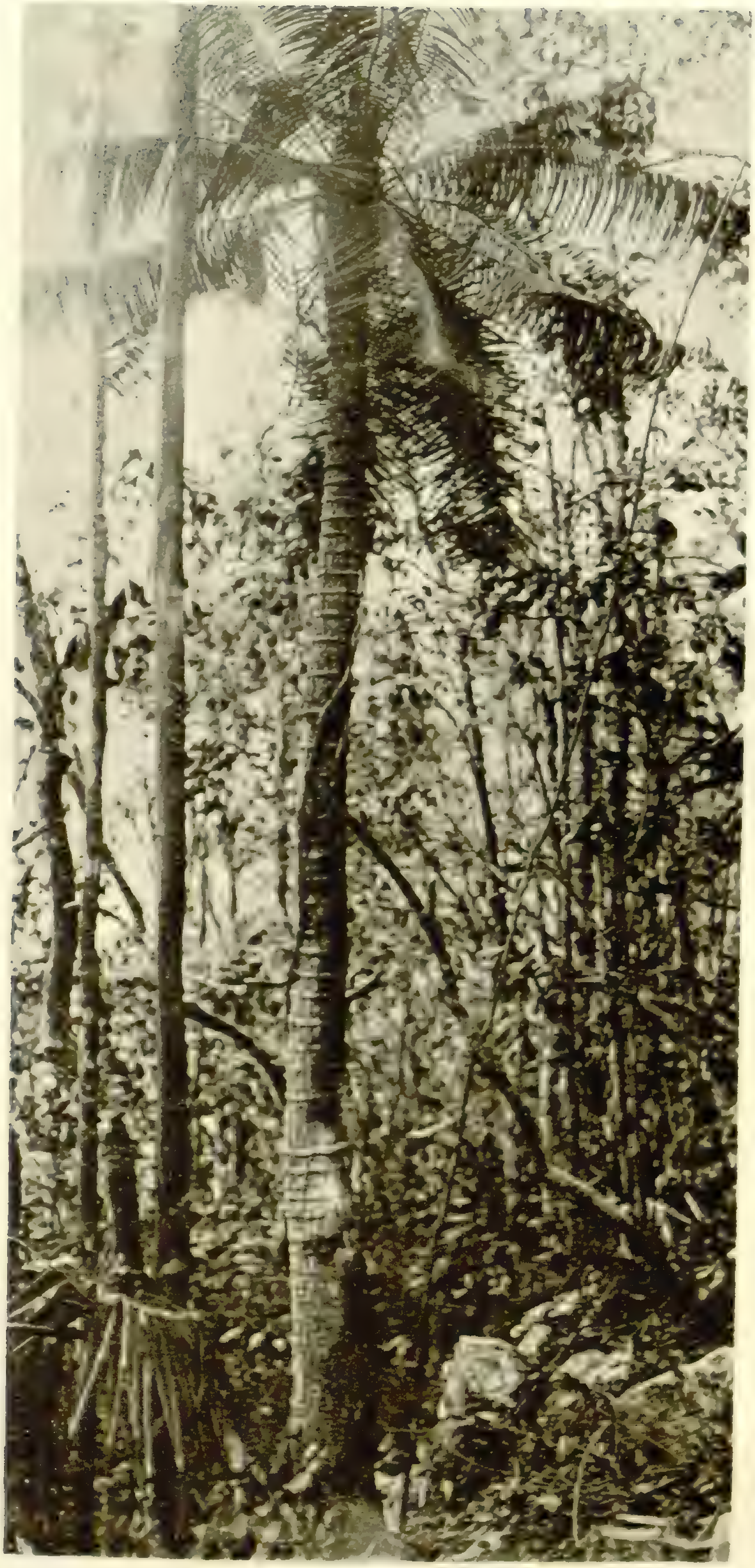

FIG. 2.—A type growing in densely shaded regions; this specimen is growing on the northern slope of a steep rocky mountain.

older ones of the shaded forms, may be seen rings of the cortex and bark which indicate the position of former terminal buds (*figs. 2, 4, 5, 6, 8*). Just what these may signify relative to age has not been determined. It may be that they are formed only by the foliage buds, or only from scale buds, or even possibly from reproductive buds, or all of these put together. It is not known how often a new crown of scales, or of foliage leaves, or of reproductive structures is formed in Microcycas. These rings may persist until the plant is quite old (*fig. 4*), or may disappear entirely and give place to a bark-formation quite resembling that of the trunk of some pines (*fig. 3*). In nearly all older plants at the base of the stem will be seen such bark-formation as shown in the figure just cited, while at some point above the characteristic rings appear. Were these characteristics not found upon the same stem, one could readily believe that the stems shown in *figs. 2* and *3* do not belong to the same species.

The details of anatomy of the stem have not been investigated. From a gross examination it is evident, however, that Microcycas has a single vascular cylinder surrounded by a thick cortex and enclosing a large pith region (*fig. 10*), as in Zamia, Dioon, and Stangeria. The pith is extremely brittle, and its cells are densely filled with very large starch grains.

The leaves, which often exceed a meter in length, vary greatly in the number in each crown (*figs. 1–8*). The length of life of a leaf could not be determined, and although no leaves upon old plants were found opening from the bud, the vernation in seedlings is circinate.

OVULATE CONES AND MEGASPORANGIA

A single ovulate cone (*fig. 8*) was found on a number of plants. It appears upon first observation to be a terminal structure, but closer investigation indicates that it is lateral, though younger material must be studied to determine definitely this point. The base of the cone is enclosed by heavy, hairy scales (*figs. 11, 12*) which usually have their upper ends pressed closely between the outer portions of the basal sporophylls. The cone shown in *fig. 8* was 94^{cm} from the center of its base to the center of its tip, and weighed 9.5^{kg}, being the largest cycad cone yet reported. This one, however, appears to be slightly larger than the average ovulate cone of Microcycas.

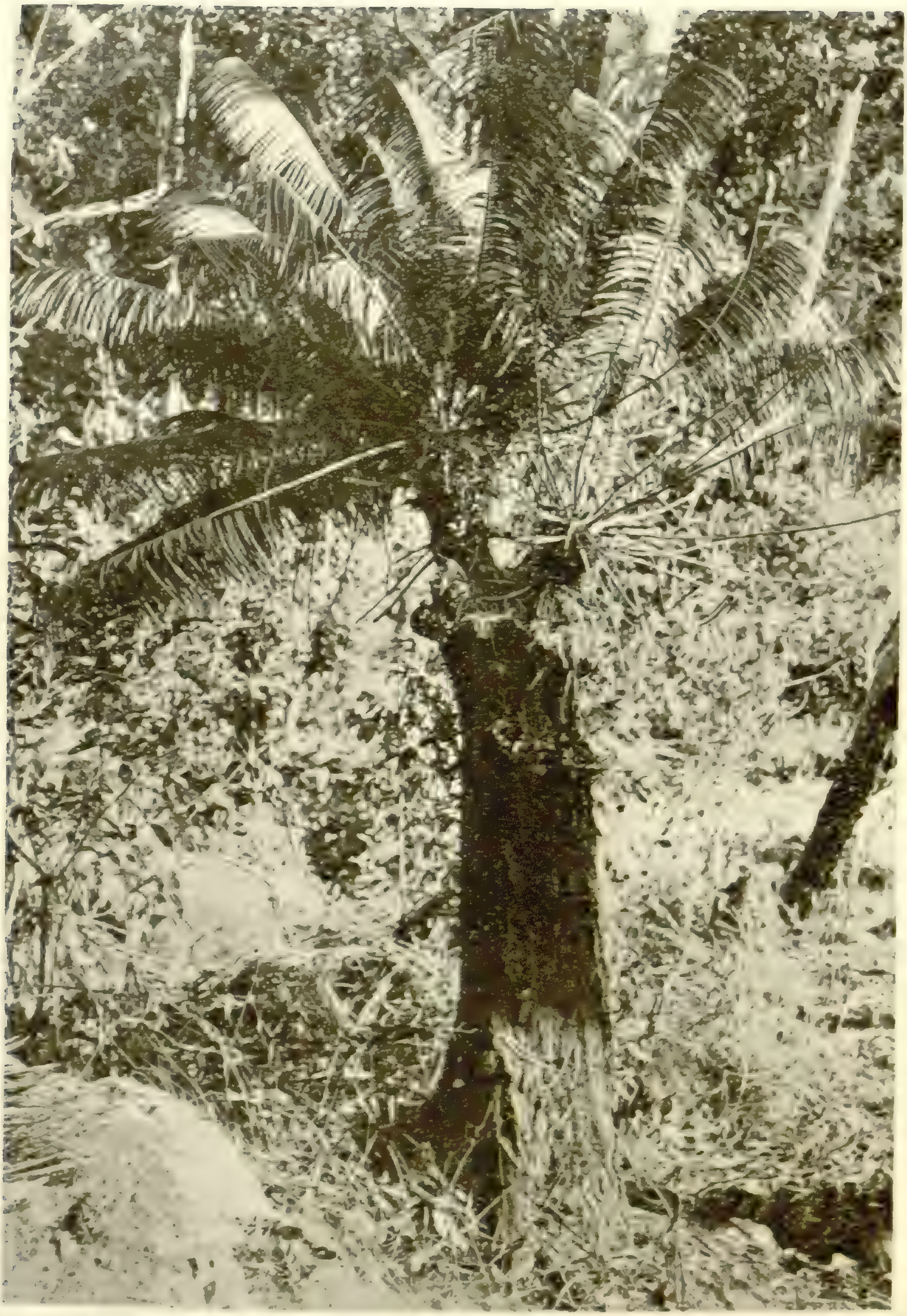

FIG. 3.—An old plant with numerous branches; rings about the stem have disappeared, and ridged bark is present.

In cones of the ages shown in the figures the sporophylls are closely pressed together, and are covered over the exposed portion by a dense mass of closely appressed grayish hairs. At the time of seed distribution the sporophylls separate, the entire cone bends on its stem, and is pendent from the apex of the plant. The individual sporophylls bear some resemblance to those of Zamia, but are specifically distinct. The outer portion is drawn out into an obtuse point, upon which are two ridges.

Most of the cones are quite symmetrical and are remarkably well rounded both at base and tip, thus suggesting complete pollination and development of sporangia (*figs. 8, 11, 12*). In some cases this is not true, and irregularities suggesting imperfect pollination are conspicuous. To the left in *fig. 11* such a cone is shown.

Each sporophyll bears two sporangia of a peculiar salmon-pink color. These sporangia in the mature cones are closely crowded together (*fig. 12*), thus producing the corklike form of the seed from which is derived the Cuban name "palma corcho." The integument of the ovule is differentiated into an outer fleshy layer; a thin, hard, brown layer; and an inner fleshy layer which becomes thin and papery. Vascular bundles pass up the stalk of the megasporophyll, anastomose in the upper portion, and give off five to eight branches which pass into each ovule. Just after entering the base of the ovule each vascular bundle forms two branches, one of which traverses unbranched the outer fleshy layer; the other enters the hard coat and divides into a large number of anastomosing branches (*fig. 16*).

STAMINATE CONE AND MICROSPORANGIA

Although the staminate cones had formed and shed their pollen some months before they were obtained, one entire cone and fragments of several others were found. It is likely that the entire cone shown in *fig. 13* was delayed in development and did not mature its pollen normally, since all the other staminate cones are pendent and had their stamens separated by elongation of the cone axis. From the material collected it would seem that the staminate cone is 25–30^{cm} long and 5–8^{cm} thick. Its position on the tip of the stem indicates that it is lateral in origin.

The microsporophyll has its outer portion expanded, and spo-

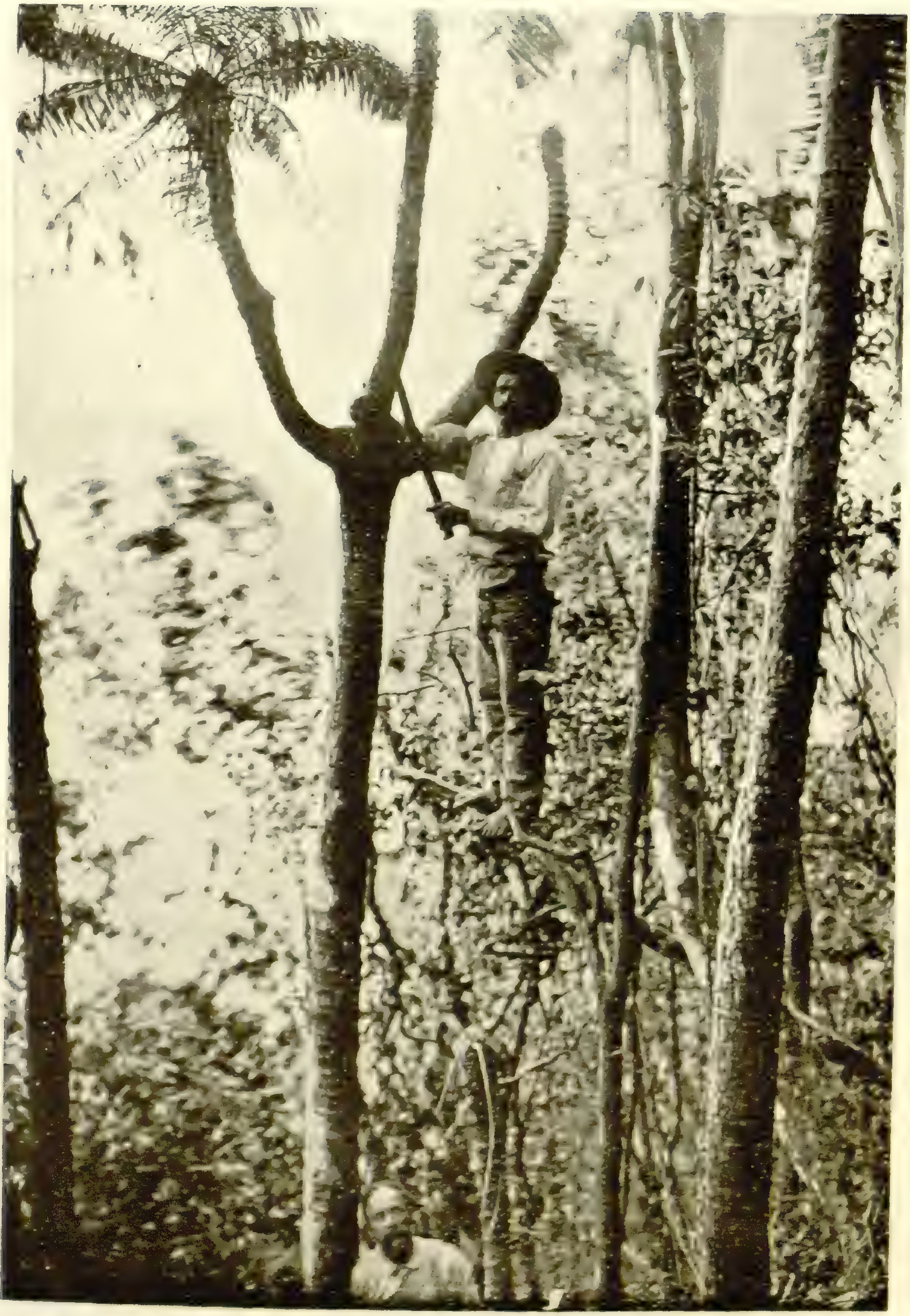

FIG. 4.—Three plants; large one at right (9.5^{m} high) showing neither crown nor base; in the middle a small plant showing terminal bud and two or three old leaf stalks; at left a branching plant, the height of which is suggested by the two men, one of whom is standing at the base of the tree.

rangia entirely cover the basal two-thirds of the abaxial surface (*fig. 14*). They are not arranged in sori and cover the basal and apical sporophylls as completely as they do those in the middle of the cone. The sporangium dehisces by a long slit which extends almost to its base. The microspores are spherical, with a moderately heavy exine and a quite prominent intine.

MALE GAMETOPHYTE AND SPERMS

None of the pollen collected could be made to germinate, possibly due to its age and to the fact that a fungus was growing in the material when collected.

In the earliest stages shown by the material, the male gametophyte is already well developed (*fig. 15*). After the microspore reaches the pollen chamber, the pollen tube grows upward and outward into the nucellus. The relation of this growth in time to the development of the structures within the tube could not be determined. In pollen tubes at this stage there are usually a tube nucleus, a prothallial cell, a stalk cell, and eight body cells (*figs. 17, 18*). The tube nucleus is usually near the tip of the tube (*figs. 18, 19*), but sometimes behind some of the body cells (*fig. 15*). Most of the body cells remain near the base of the pollen tube, though some are usually near its tip. While the number of body cells is most frequently eight, it varies to nine (*fig. 20*), ten (*fig. 19*), and possibly more. Several illustrations of such variation were found.

The prothallial cell extends into the stalk cell (*figs. 17–20*), as described by WEBBER (**6**) in Zamia. At the base of the prothallial cell there may be seen sometimes a darkly staining mass which may possibly be the remnant of a first prothallial cell (*figs. 19, 20*).

In the youngest body cell observed the two blepharoplasts are well organized, each with numerous radiating lines of cytoplasm which extend well down toward the equator of the cell (*fig. 21*). The nucleus is sometimes irregular in form, as if its membrane in places were being pushed inward by the cytoplasmic radiations. When the nucleus varies from the spherical form, it is more or less flattened at right angles to the lines of radiating cytoplasm (*figs. 17–20, 21, 47*). At this stage the blepharoplasts are usually opposite each other, and the entire cell presents a beautiful symmetrically arranged spherical figure. A few cases were observed in which the blepharoplasts were near each other (*figs. 22, 23*), and one case in which they were in contact (*fig. 24*); a careful search failed to show other blepharoplasts. WEBBER figures similar cases, except he found none in which the blepharoplasts were so close together as in *figs. 23* and *24*.

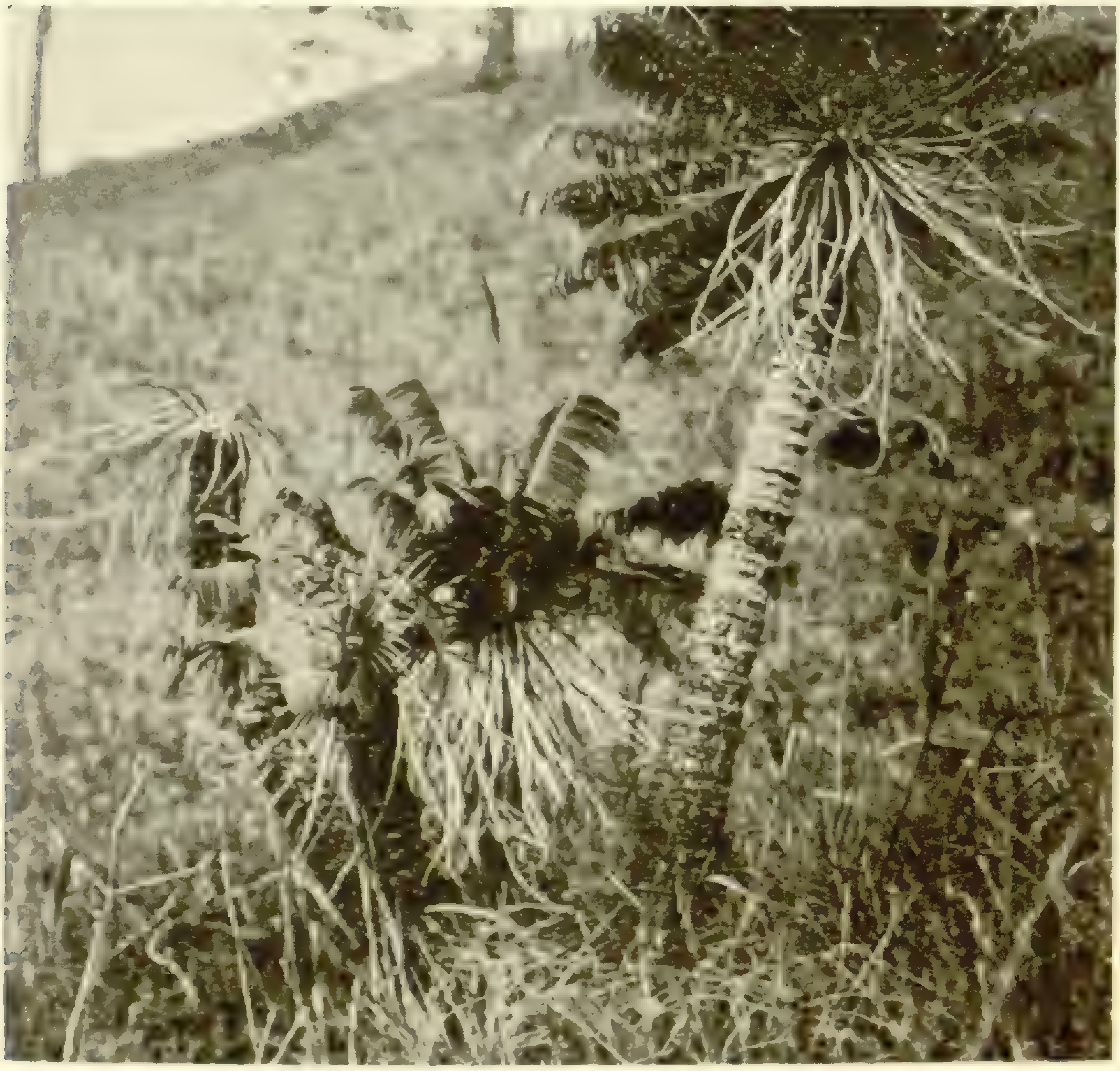

FIG. 5.—Four plants which have grown from stump of an old plant; an exposed grassy hillside.

The division of the body cell (*fig. 25*) results in the formation of two sperm mother cells, which become separated by a definite wall (*fig. 27*). While this division is occurring, the blepharoplasts begin to form a distinct band (*fig. 25*); later this band may become broken up into fragments or small granules, upon which the beginnings of the cilia may be seen (*fig. 27*). The mother cell does not become spherical, but is flattened on the side adjoining its mate, and when somewhat older than the stage shown in *fig. 27* is distinctly beaked at the end, where most of the blepharoplast granules lie. This nuclear beak is described for Cycas by IKENO (7), but according to WEBBER'S figures it does not occur in Zamia. The sperm cells nearly always

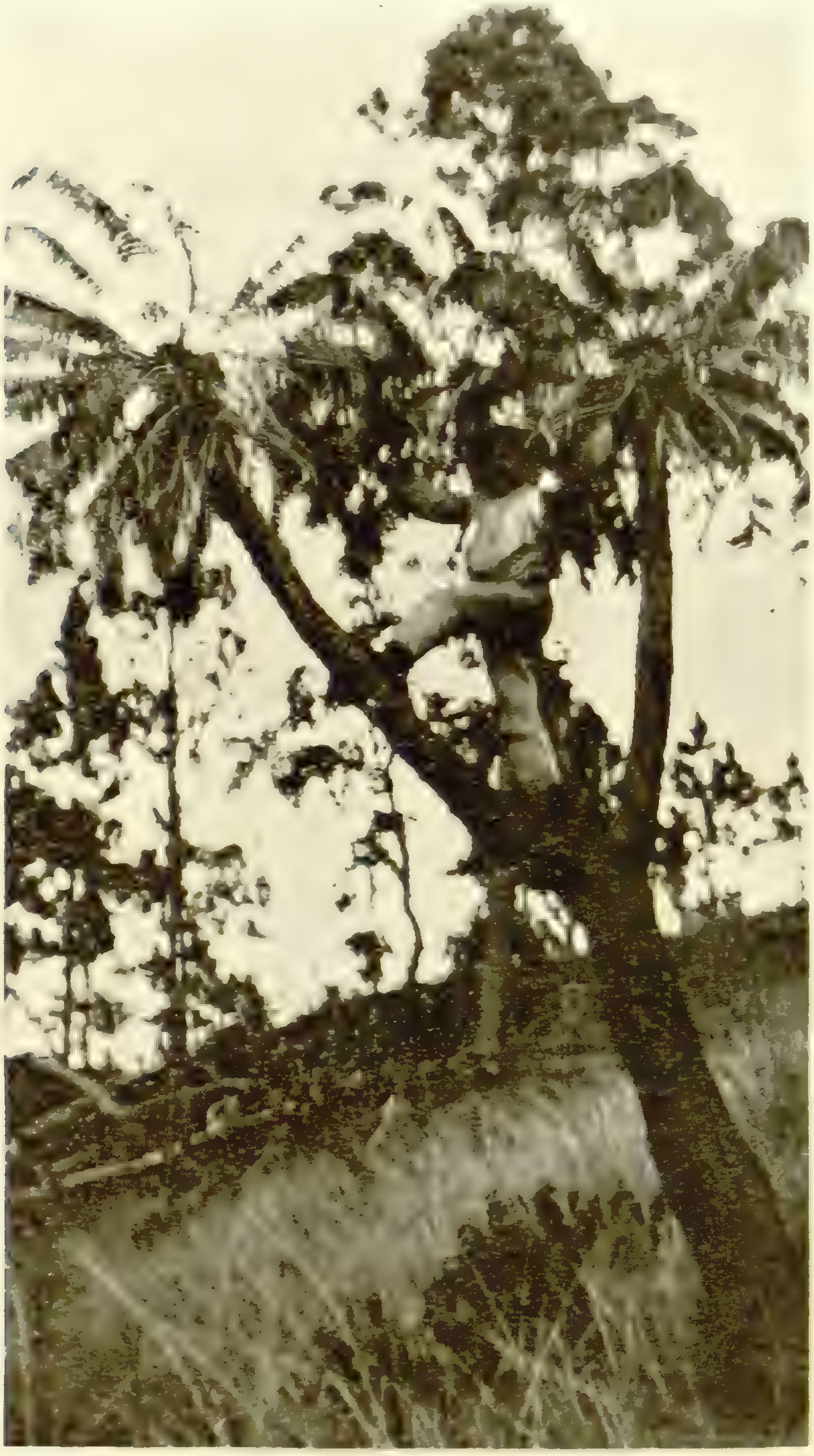

FIG. 6.—A tall branching plant growing in the open and having much the same form as those found in densely shaded areas.

become entirely free from one another before the ciliated band is formed. In Zamia WEBBER points out that the ciliated band is formed before the mother cells become separate, and describes one case in which he observed two sperms swimming while yet attached to each other.

In this manner sixteen sperms are formed in each pollen tube (*figs. 28, 29*). In those pollen tubes in which nine or ten (or possibly more) body cells are formed, it is probable that a larger number of sperms is formed, but no case was observed in which there were more than sixteen sperms.

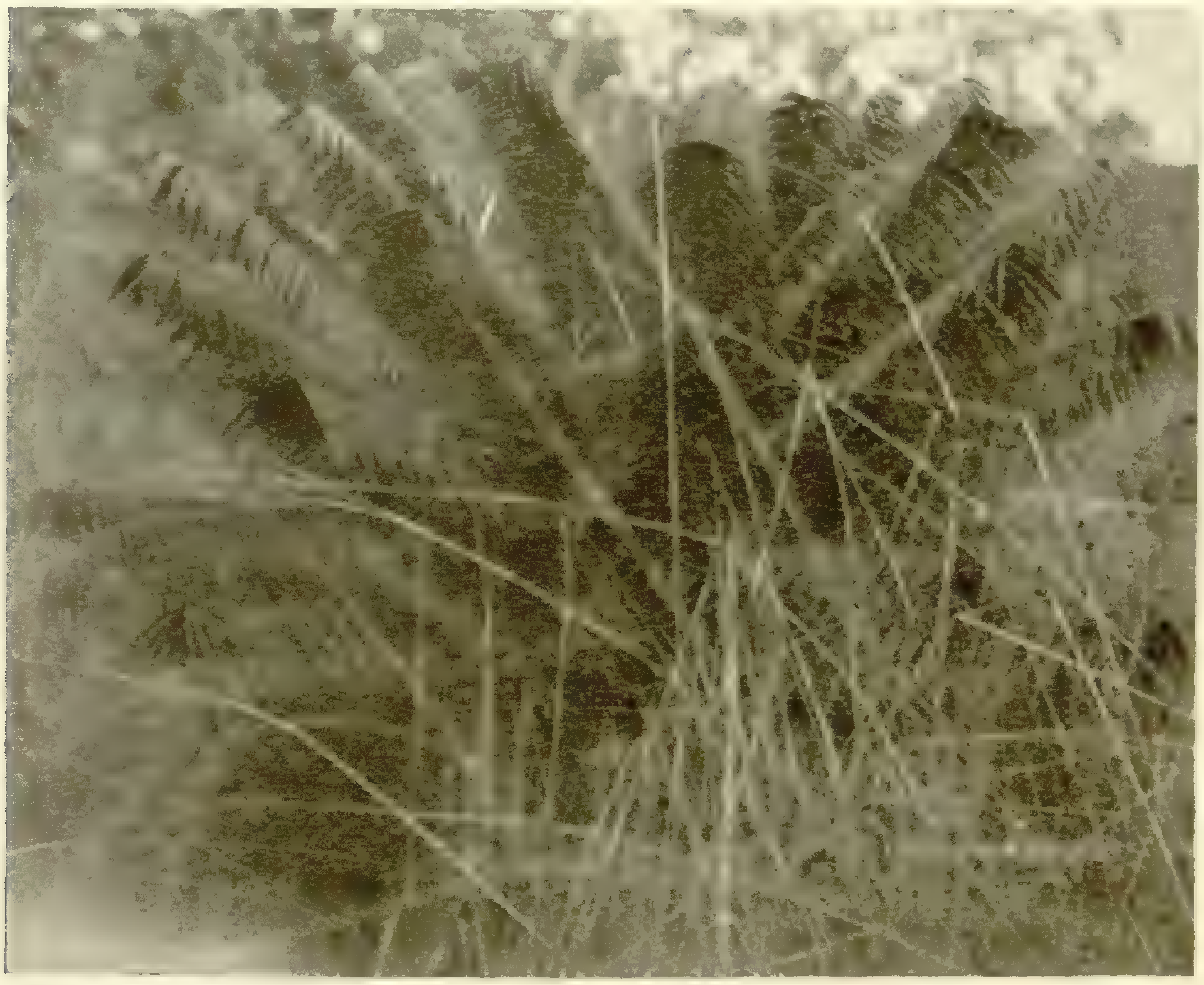

FIG. 7.—A young plant of the type usually found in exposed regions. The crown of such plants suggests that of *Cycas revoluta*.

When the body cells begin to divide to form the mother cells, the tube grows toward the female gametophyte (*fig. 26*). In one case the entire mass of sperms was formed within the thicker portion of the intine, at the point where the pollen tube began to develop from the microspore (*fig. 29*). Whether in this particular case there had been an upward growth of the pollen tube could not be determined. Usu ally the downward growing branch of the tube in which the mass of sperms is found is thin-walled, as are the ascending and lateral branches (*fig. 28*). By dissecting pollen tubes from a cone that had been kept in the laboratory for two months, motile sperms were observed; the general form is shown in *fig. 30*. So far as could be determined, their behavior was similar to that of the sperm described

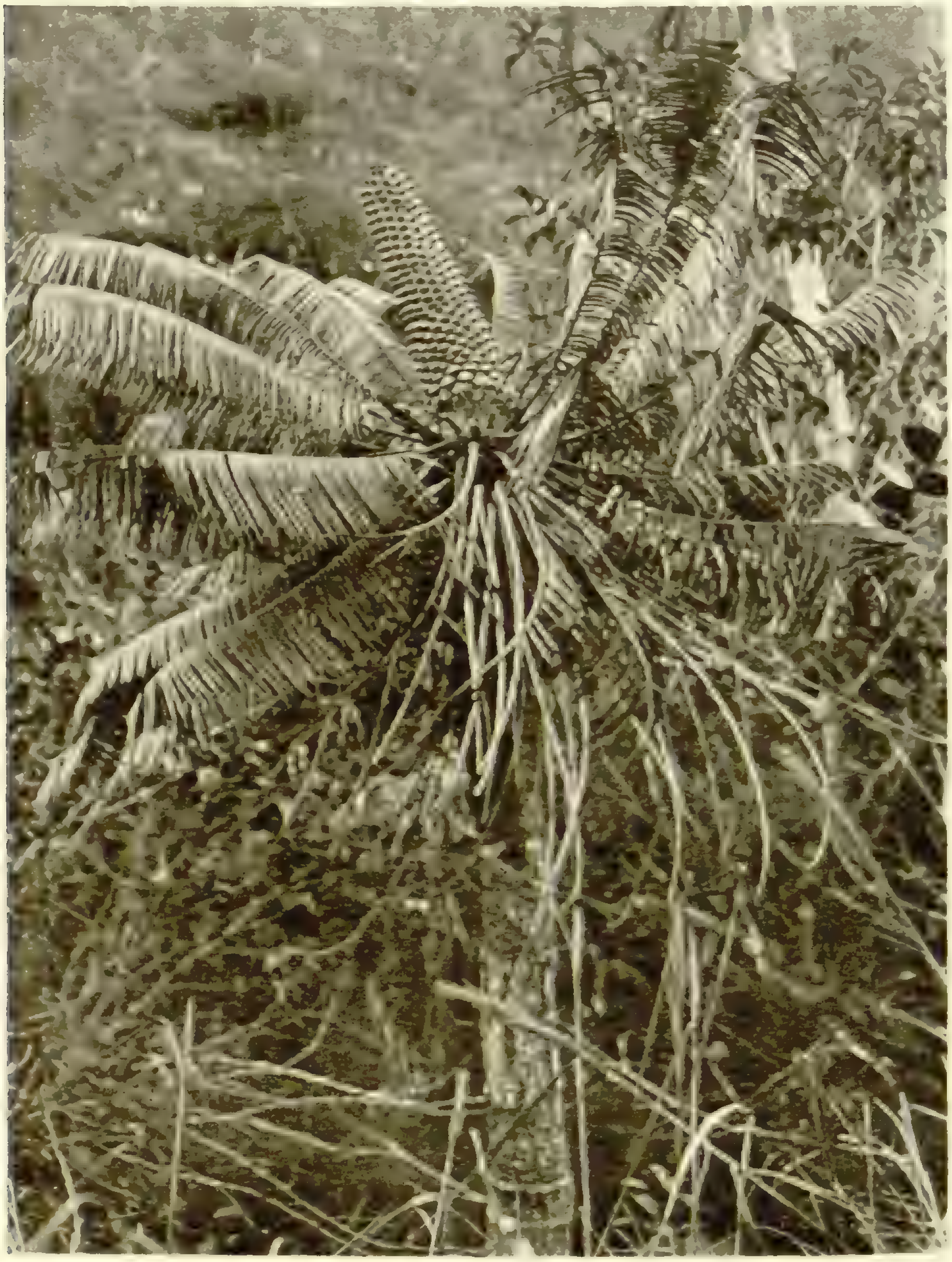

FIG. 8.—An ovulate cone growing upon a plant which stands in a ravine.

for Cycas by **Ikeno**, for Ginkgo by **Hirasé** (8), for Zamia by **Webber**, and for Stangeria by **Lang** (9). The cone had lost its vigor, however, and no cases of fertilization were secured.

The full significance of this remarkable number of sperms in each male gametophyte cannot be known without an investigation of the origin of the body cells. No other seed-plant has been found to have more than two male cells in each male gametophyte. The fact that there are in Microcycas sixteen mother cells, each organizing a sperm, is especially suggestive when it is recalled that a common number of sperms in each antheridium of the leptosporangiate ferns is thirty-two. Another division of the body cells of Microcycas would result in this fern condition. It will be of great interest to know whether any of the four cycad genera as yet uninvestigated possess this remarkable character.

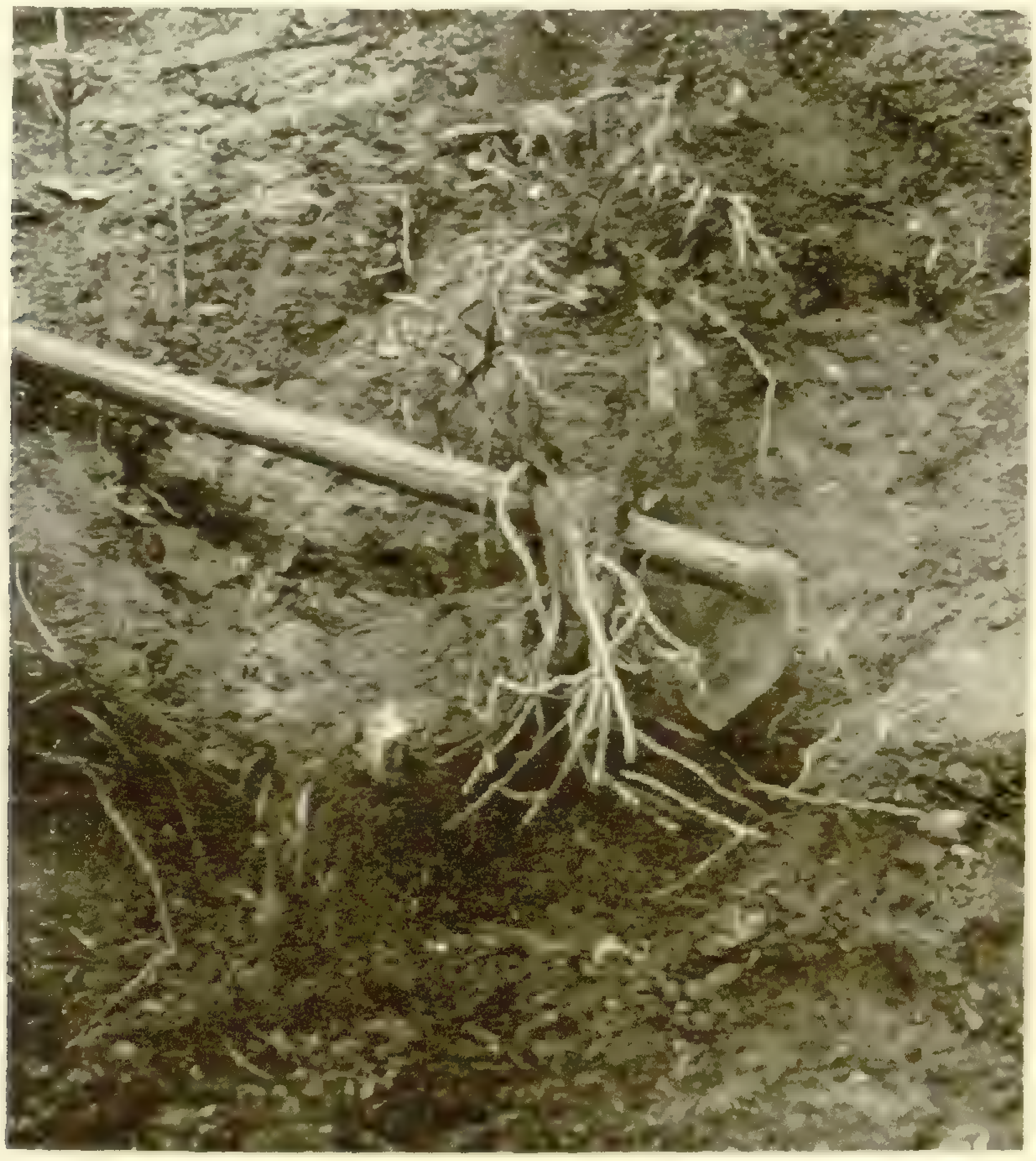

Fig. 9.—A relatively young plant removed from the earth.

FEMALE GAMETOPHYTE AND ARCHEGONIA

None of the material was sufficiently young to show stages in the development of the female gametophyte. The structure of the adult gametophyte, however, shows that tissue-formation proceeded in the usual centripetal manner. Usually the radial arrangement of the cells is quite evident (*fig. 48*), and in nearly all cases there is a median line formed by the abutting tissues (*fig. 50*); in some cases this median cleft extends to the micropylar end of the gametophyte. On the surface of the gametophyte the tissue often produces lobes, between which there may be conspicuous seams of more or less completely united tissues running well into the interior of the gametophyte (*fig. 50*). It seems probable that these lobes continue to grow outward after the main body of the gametophyte is well formed. The cells of the gametophyte are well filled with starch. The entire structure

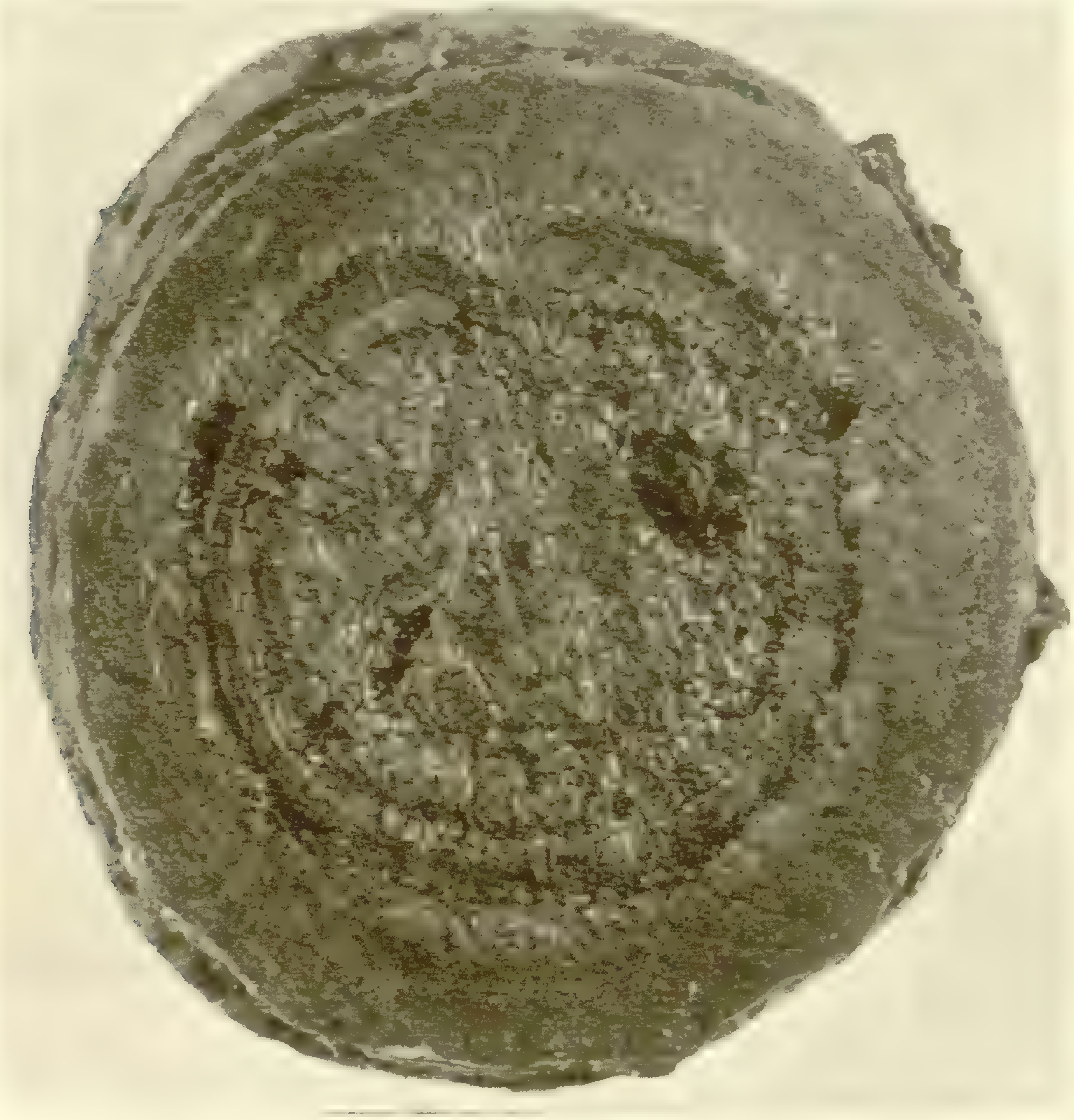

FIG. 10.—Cross-section of stem.

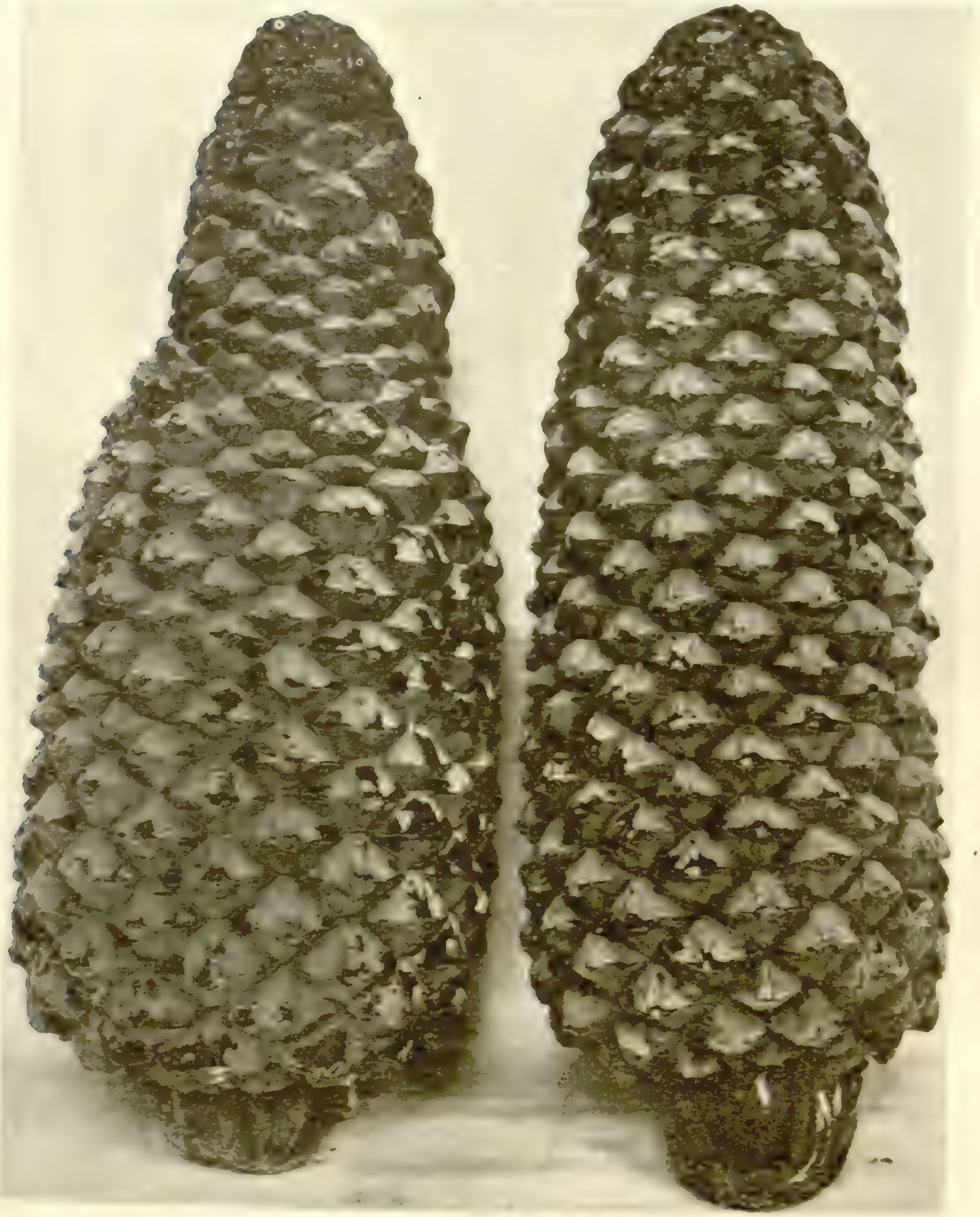

FIG. 11.—Two ovulate cones.

is 2.5–3.5^{cm} long and 1.75–2^{cm} broad. The nucellus forms an extremely thin layer closely adhering to the surface of the gametophyte.

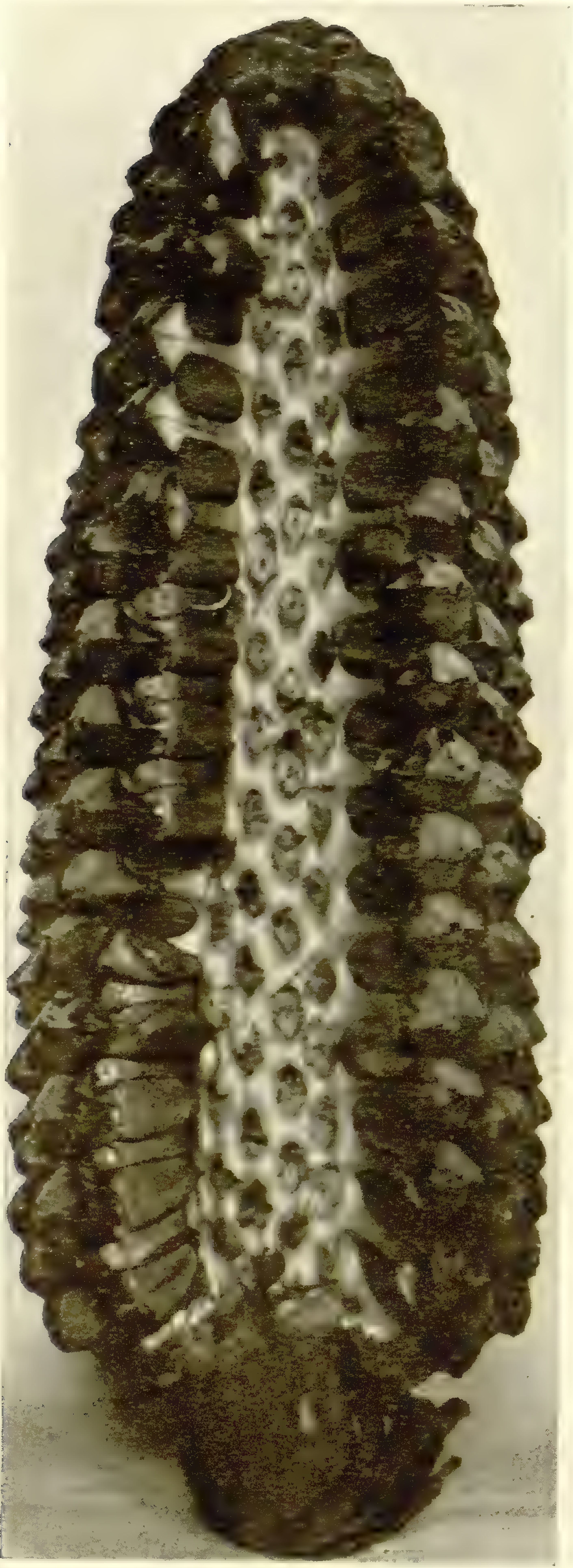

FIG. 12.—An ovulate cone; some of the sporophylls have been removed, showing the central axis and the attachment of the ovules.

Archegonia may be formed at the micropylar end of the gametophyte, or on the lobes produced on the sides or lower end, or on the unlobed surface, or in rare cases within the tissues in such position as to open to the median cleft (*figs. 32, 48, 49, 50*). They are more abundant at the micropylar end than elsewhere, and in many cases they are formed in no other region (*fig. 48*). The number of archegonia is large; one cross-section made a little back of the end of the gametophyte showed 169 distinct archegonia. Doubtless in many cases the number exceeds 200 in the entire gametophyte and may even be double that number (*fig. 49*). There is apparently little difference in the age of archegonia at the micropylar end and on the lateral lobes.

The age of the material did not permit a study of the development of the archegonium. Two neck cells are formed, but these do not protrude as noted in Zamia by COULTER and CHAMBERLAIN (**10**), and in Dioon by CHAMBERLAIN (**4**); they may extend slightly beyond the surface of the gametophyte (*fig. 33*), but usually they are even with the surface, as shown in the case of the single neck cell in *fig. 34*. In some cases at least, the neck cells break down, leaving the central cell exposed at the surface of the gametophyte (*figs. 35, 36*). The contents of the archegonia showed considerable variation. In such archegonia as are shown in *figs. 33* and *34*, there is the usual condition in which the ventral canal cell has not yet been cut off; in numerous other cases, however, two or three nuclei were found (*figs. 36, 37, 39*). COKER (**11**) found that in Taxodium the free ventral canal nucleus after fertilization divides amitotically; and in Podocarpus he observed (**12**) the same phenomenon. It is possible that some of the nuclei found in the archegonium of Microcycas may have arisen in this way, but failure to find any ventral canal nuclei in the usual position, though many central cells were examined, indicates that the material was not old enough to have formed ventral canal cells. That some of the central cells were almost ready to divide, hower, is shown by the condition of the nuclei in *figs. 34* and *35*. It is probable that archegonia may unite by the absorption of their dividing walls, for they often crowd upon one another very closely, as in *fig. 38*, in which absorbtion of the separating walls would result in just such a condition as is shown in *figs. 36, 37*, and *39*. Comparison with other cycads would also suggest that the archegonium has not reached the stage for cutting off the ventral canal nucleus. It seems altogether probable that a ventral canal nucleus is cut off subsequently, and that the two or more free nuclei observed are the result of the union of two or more archegonia.

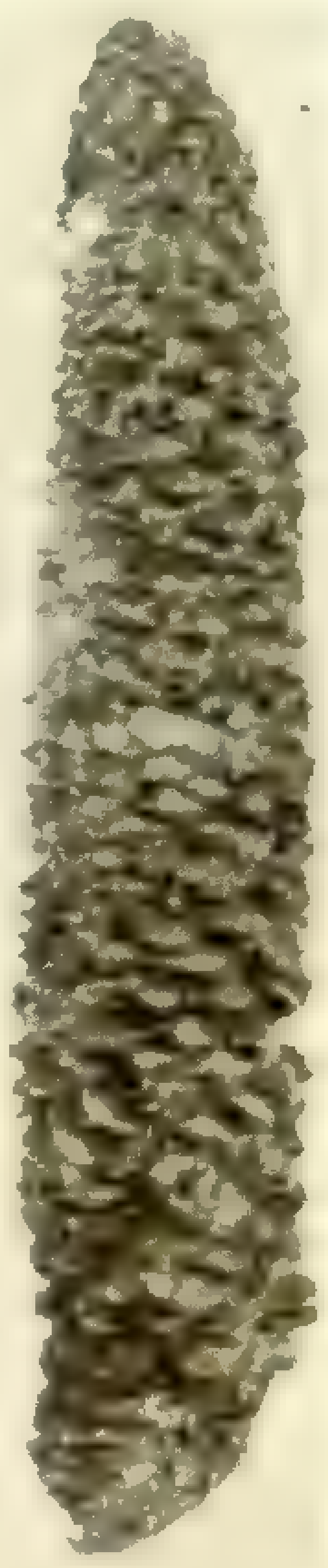

FIG. 13.—An old staminate cone.

The development of jacket cells, as described by GOROSCHANKIN (**13**), TREUB (**14**), IKENO (**7**), SMITH (**15**), STOPES and FUJII (**16**), is much less regular in Microcycas than in the other cycads studied. This is probably due to the crowding together of archegonia and the consequent absorption of intervening tissue.

The very large number of archegonia and their peculiar distribution are suggestive of primitive conditions, and this is emphasized by association with the large number of sperms.

EMBRYO

From the material collected during January and February no cases of fertilization or young embryos were found. A second collection of cones forwarded late in February failed to arrive. In a third collection, which was shipped from Cuba early in April, the ovules were found to contain embryos in which the suspensors were well developed. The suspensors are long and more or less spirally coiled (*figs. 40, 41*), the one shown in *fig. 41* being 8^{cm} long. A dozen or more embryos may be found in a single gametophyte. The pressure of the spiral suspensor is such as frequently to lift the nucellar cap when the hard seed coat is removed. Such a pressure on the embryo would hold it firmly against the endosperm. Frequently suspensors pass upward through the archegonia and over the gametophyte under the nucellar cap (*fig. 41*). No embryos were found in any archegonia except those at the micropylar end of the gametophyte.

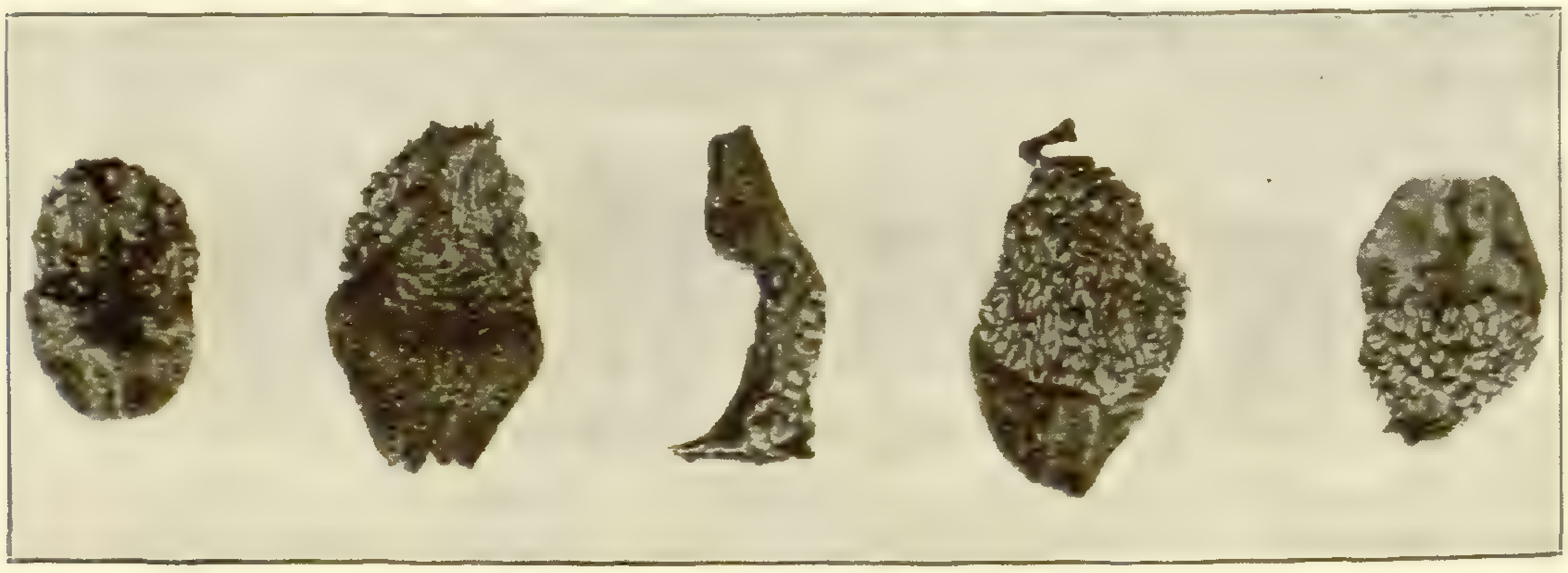

FIG 14.—Staminate sporophylls; the two at the left show the adaxial surface, the two at the right the abaxial surface, the middle one a lateral view.

While material was being collected in January and February, seeds were found on the ground at the bases of plants that had ripened ovulate cones the preceding year, and some of them had germinated. The fleshy seed coat was gone, and in many cases there were scars upon the hard seed coat, evidently made by the teeth of animals; in some cases the empty seed coat appeared to have been opened by animals.

Within the mature seed a single large straight embryo extends along the median axis. One-half is made up of the cotyledons, those in the seeds examined varying from three to six in number; usually they are straight, but occasionally they are spirally twisted (*fig. 42*). The seeds and seedlings secured were planted in the greenhouse and are just now beginning to grow. After the root tip emerges and enters the earth (*fig. 43*), the cotyledons remain in the seed coat for a long period, but its length was not determined. A tuberous stem several centimeters in length is produced before other structures emerge from the seed. The first true leaf, just now appearing in the greenhouse material, is somewhat circinate, distinctly hairy, and arises almost from the center of the stem (*figs. 44, 45*). In the peculiarly severe conditions in which Microcycas lives, there is often great danger to the seedlings of dessication, and the production of a stout tuberous stem before the production of leaves is evidently of great advantage.

SUMMARY

1. Small and widely separated groups of *Microcycas calocoma* occur in some of the mountains of western Cuba.

2. The adult plant is a small tree, and reaches the greatest height and circumference yet recorded for any cycad indigenous to the western hemisphere. The stem may be a straight shaft or may branch many times.

3. The ovulate cone is the largest known; and it and its sporophylls bear more resemblance to those of Zamia than to those of other cycads.

4. Unbranched vascular bundles pass up the stalk of the megasporophyll, anastomose in the expanded portion, then give off five to eight branches to each ovule. Immediately after entering the ovule each branch divides, one subdivision passing unbranched through the fleshy layer, and the other passing into the hard layer and branching many times.

5. The staminate cone is long and slender, and two-thirds of the abaxial side of its sporophylls is densely covered by sporangia which do not show any distinct grouping into sori.

6. In the male gametophyte eight body cells are formed and sixteen sperms. Each body cell has two large blepharoplasts which usually lie on opposite sides of the cell, but sometimes may lie side by side. Sometimes nine or ten body cells are produced.

7. The female gametophyte is often prominently lobed, and develops a large number of archegonia (sometimes exceeding 200), which are produced on any part of the surface or even within the endosperm.

8. Many embryos are produced, the suspensor being very long and spirally coiled and pressing the embryo tip against the endosperm; the cotyledons are three to six in number.

9. Microcycas may be regarded as the most primitive cycad yet described.

I wish to acknowledge the kindly assistance in the field and in camp from Señor DON FELICE HERNANDEZ Ỳ CRUZ of Santa Catalina, Cuba; assistance in the field and courtesies in the laboratories of the Cuban Agricultural Experiment Station from Professor C. F. BAKER, Director J. T. CRAWLEY, Mr. H. A. VAN HERMANN, and Mr. E. W. HALSTED; and courtesies of the laboratories, constant suggestions, and helpful criticism from Professor JOHN M. COULTER and the members of the botanical staff of The University of Chicago.

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EXPLANATION OF PLATES X–XIII

PLATE X

FIG. 15. Diagram of nucellus showing haustorial branches of pollen tubes growing upward and outward from pollen chamber. ×15.

FIG. 16. Diagram of megasporophyll showing anastomosing of veins in expanded portion; veins passing into ovule and rebranching at base of ovules into outer fleshy and stony layers: *g*, female gametophyte; *n*, nucellus; *i*, stony layer; *v*, unbranched vascular bundle in fleshy layer (*o*); v^1, branching vascular bundles in stony layer. ×$\frac{2}{5}$.

FIG. 17. Pollen tube containing eight body cells, some of which show two blepharoplasts; one small tube nucleus; stalk cell and projecting into it the prothallial cell; a fragment of the exine adheres to the intine at the base of the tube. ×160.

FIG. 18. Pollen tube with eight body cells, tube nucleus, stalk cell, and prothallial cell. ×160.

FIG. 19. Pollen tube at left of *fig. 15;* contains ten body cells and the other structures shown in *figs. 17* and *18*. ×160.

FIG. 20. Pollen tube containing nine body cells. ×160.

PLATE XI

FIG. 21. Body cell surrounded by thin layer of cytoplasm; blepharoplasts at opposite ends of the cell; nucleus apparently compressed by radiating fibers; prominent nucleolus. ×750.

FIG. 22. Blepharoplasts on same side of body cell. ×1400.

FIG. 23. Blepharoplasts near one another. ×1400.

FIG. 24. Blepharoplasts in contact. ×1400.

FIG. 25. Spindle in body cell, showing some of the chromosomes; blepharoplasts beginning to form band. ×750.

FIG. 26. Diagram of nucellus showing several pollen tubes; lowest one showing the descending portion in which the sixteen sperms are formed. ×15.

FIG. 27. Pair of mother cells formed from body cell; near wall may be seen fragments of blepharoplasts. ×750.

PLATE XII

FIG. 28. Descending tip of pollen tube in which are fifteen sperms in process of formation; top of spiral of one is shown, and the beginnings of spiral bands in two others; to the left is the tube nucleus. ×450.

FIG. 29. Pollen tube containing sixteen sperms, two of which show merely the tip of their spiral bands; it was not possible to discover in this tube the usual haustorial branch that ascends into the nucellus, all development having apparently taken place almost within the limits of the old microspore; intine unusually heavy and somewhat broken; growth in the direction of the archegonia. ×180.

FIG. 30. Sperm seen from above. ×750. (Plate XI.)

FIG. 31. Part of ciliated band showing two regions and cilia arising from darker one. ×1400.

FIG. 32. Diagram of cross-section of ovule, made from cross-section about one-third its length from micropylar end. ×3.

FIG. 33. Diagram of an archegonium. ×75.

FIG. 34. Archegonium, showing central cell and one neck cell.

FIG. 35. Tip of archegonium; neck cells absent or broken down. ×750.

FIG. 36. Archegonium containing three nuclei, probably resulting from union of three archegonia; neck cells absent or broken down. ×750.

FIG. 37. Archegonium containing three nuclei, probably resulting from union of three archegonia. ×270.

FIG. 38. Diagram of section of two archegonia, the two having the form of one, but still separated by wall. ×270.

FIG. 39. Cross-section of an archegonium containing two nuclei. ×270.

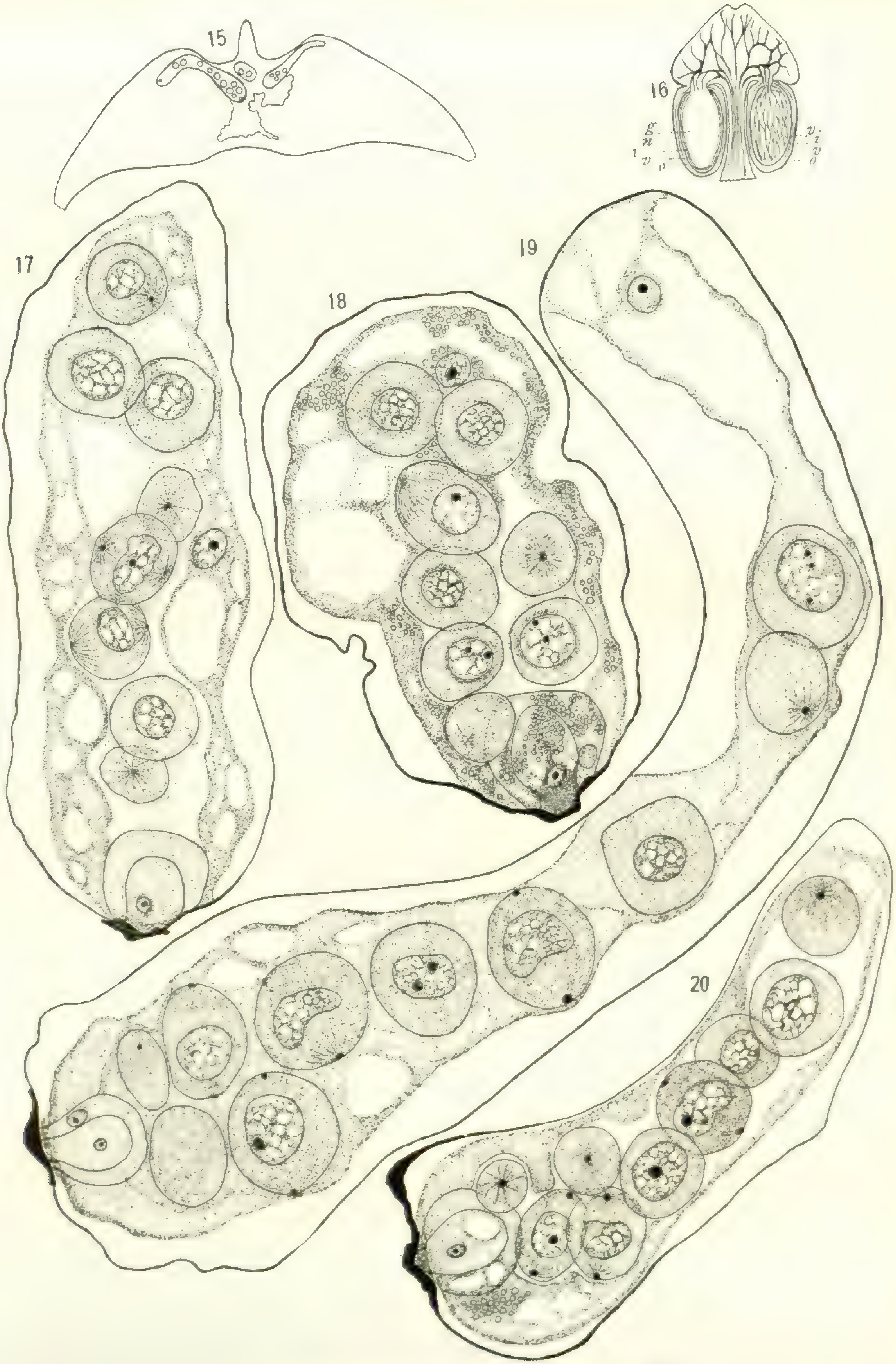
FIG. 40. Two young embryos, their suspensors so closely attached as to be indistinguishable above, but separated below; at top is mass of old archegonia from one of which the embryos are growing. ×2.

FIG. 41. Older embryos growing from mass of old archegonia; the longest suspensor measured 8^{cm} in length; two suspensors growing upward from the archegonia were closely appressed to the gametophyte immediately beneath the nucellar cap. ×½.

FIG. 42. Endosperm (seed coats removed) containing an embryo; cotyledons spirally twisted, a feature not present in most seeds examined. ×½.

FIG. 43. Germinating seed. ×½.

FIG. 44. Young plantlet resuming growth after having been transplanted; stem in same position as found in nature; at its top are scale-like growths which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CALDWELL on MICROCYCAS

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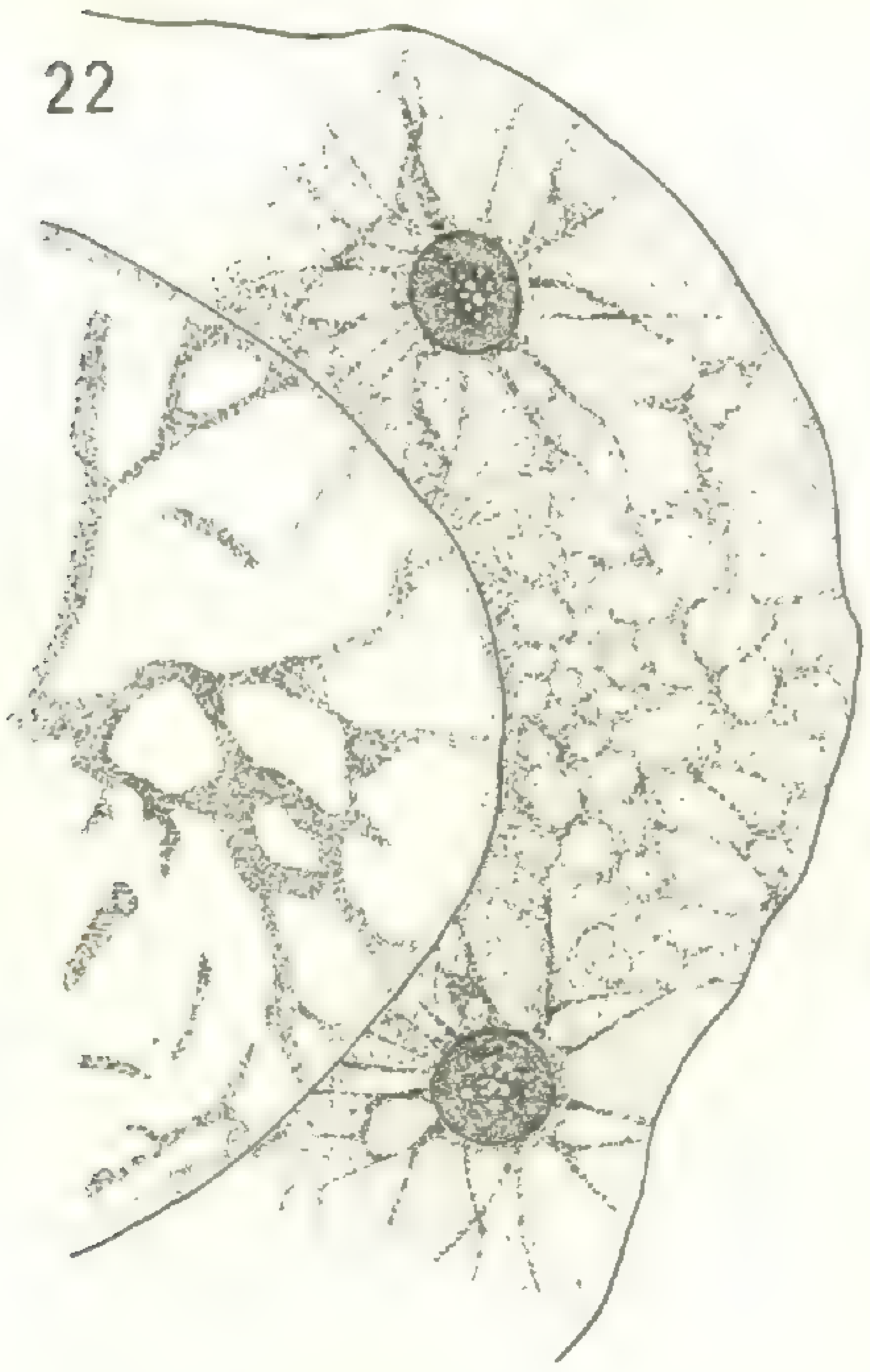

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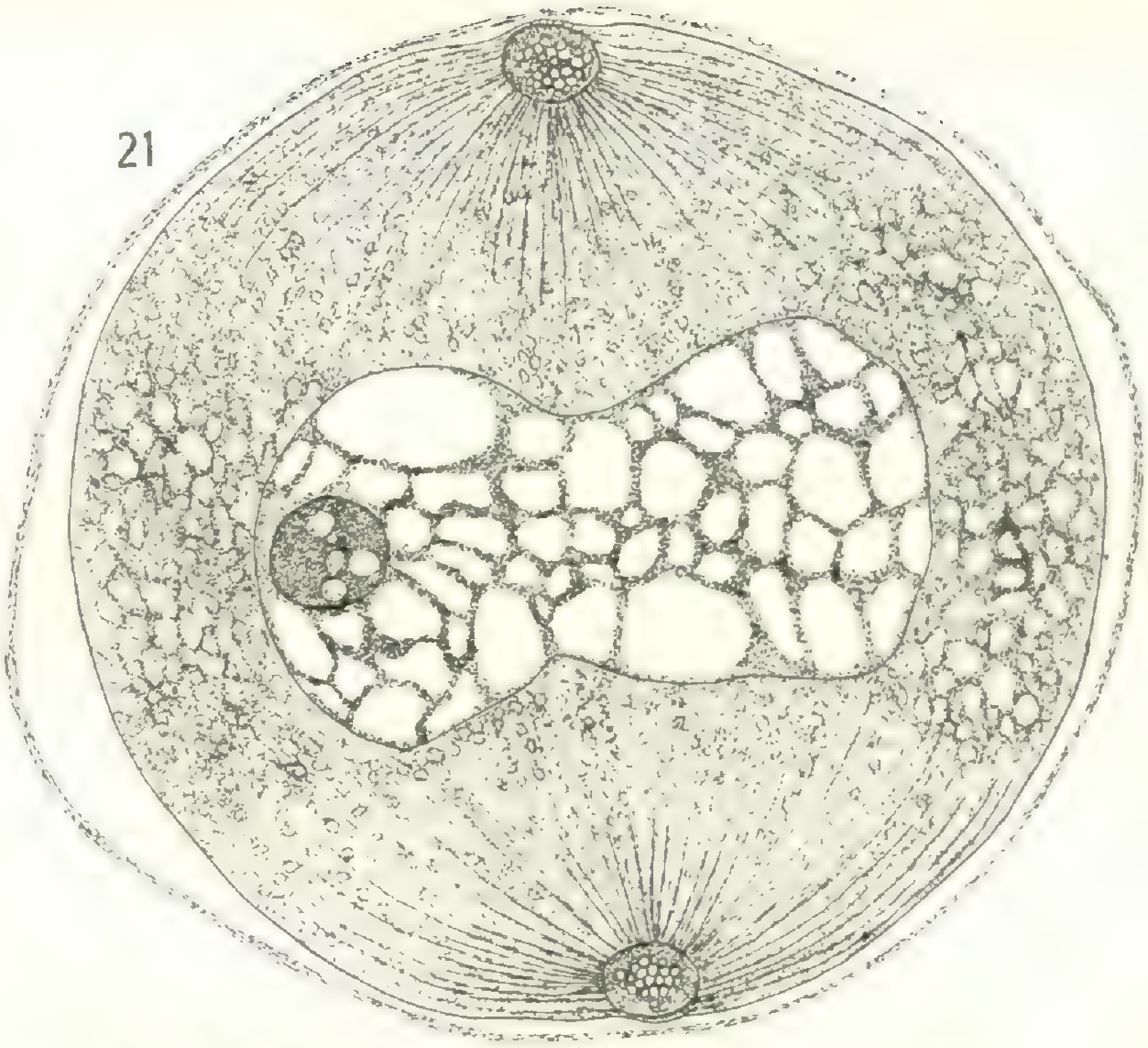

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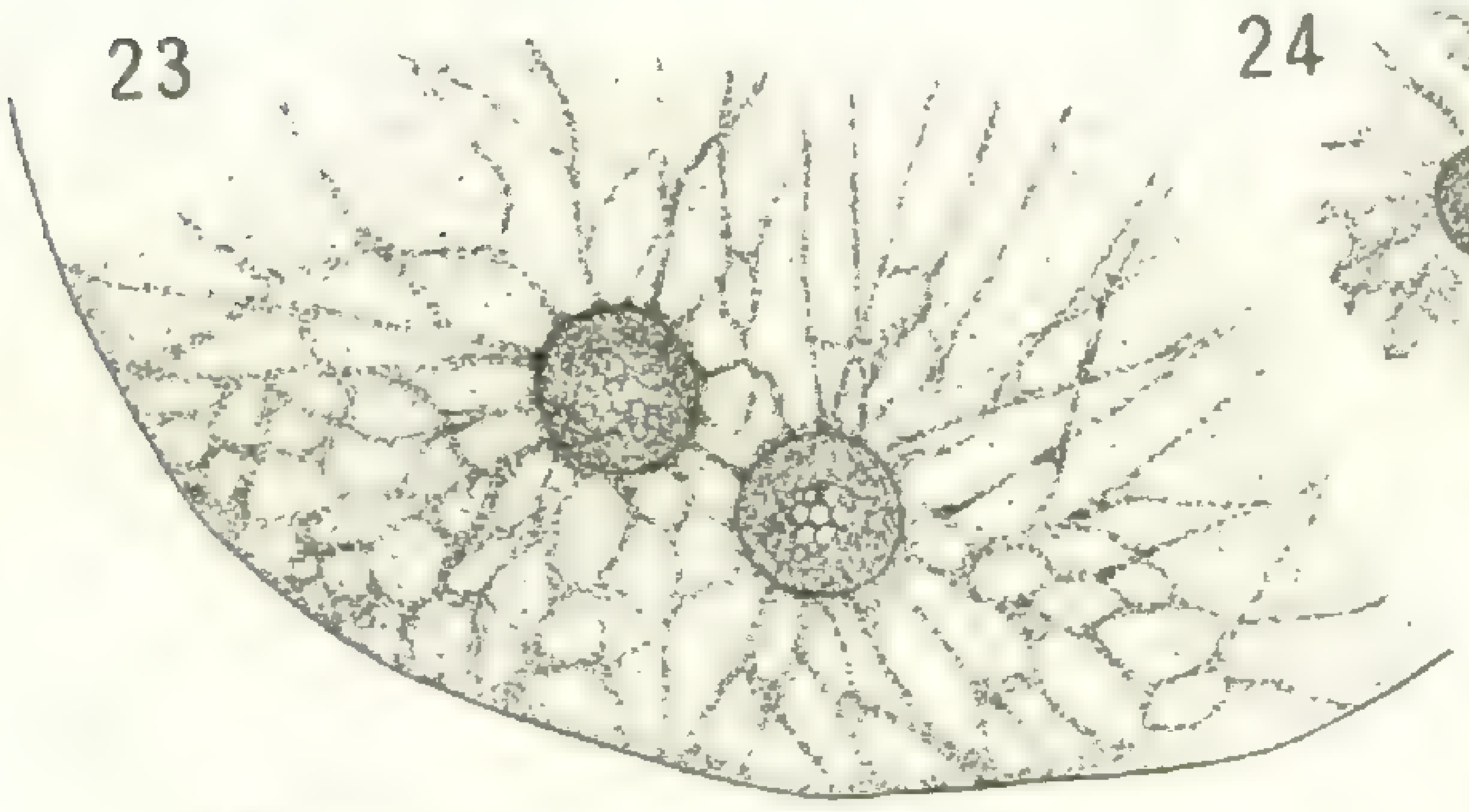

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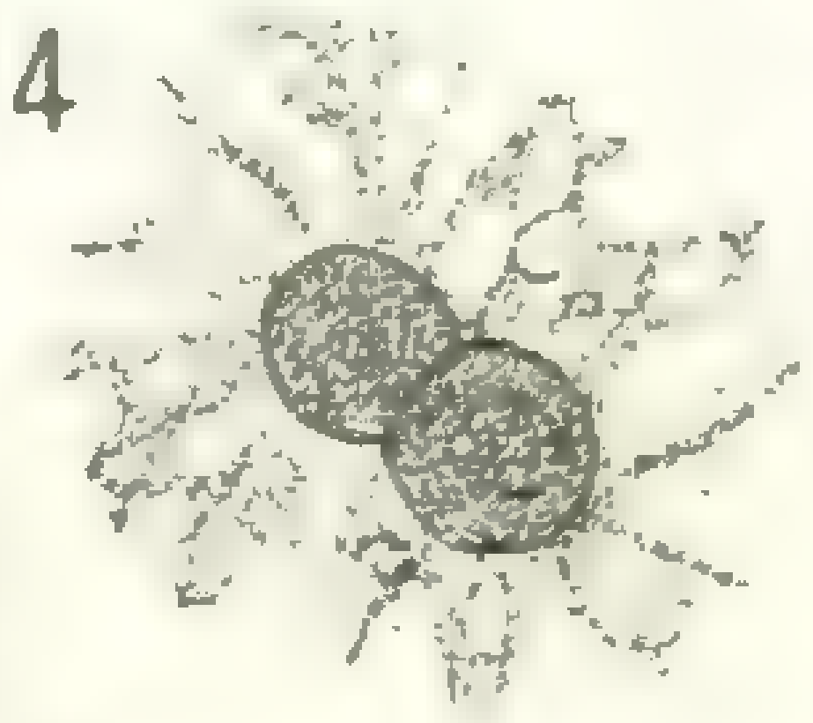

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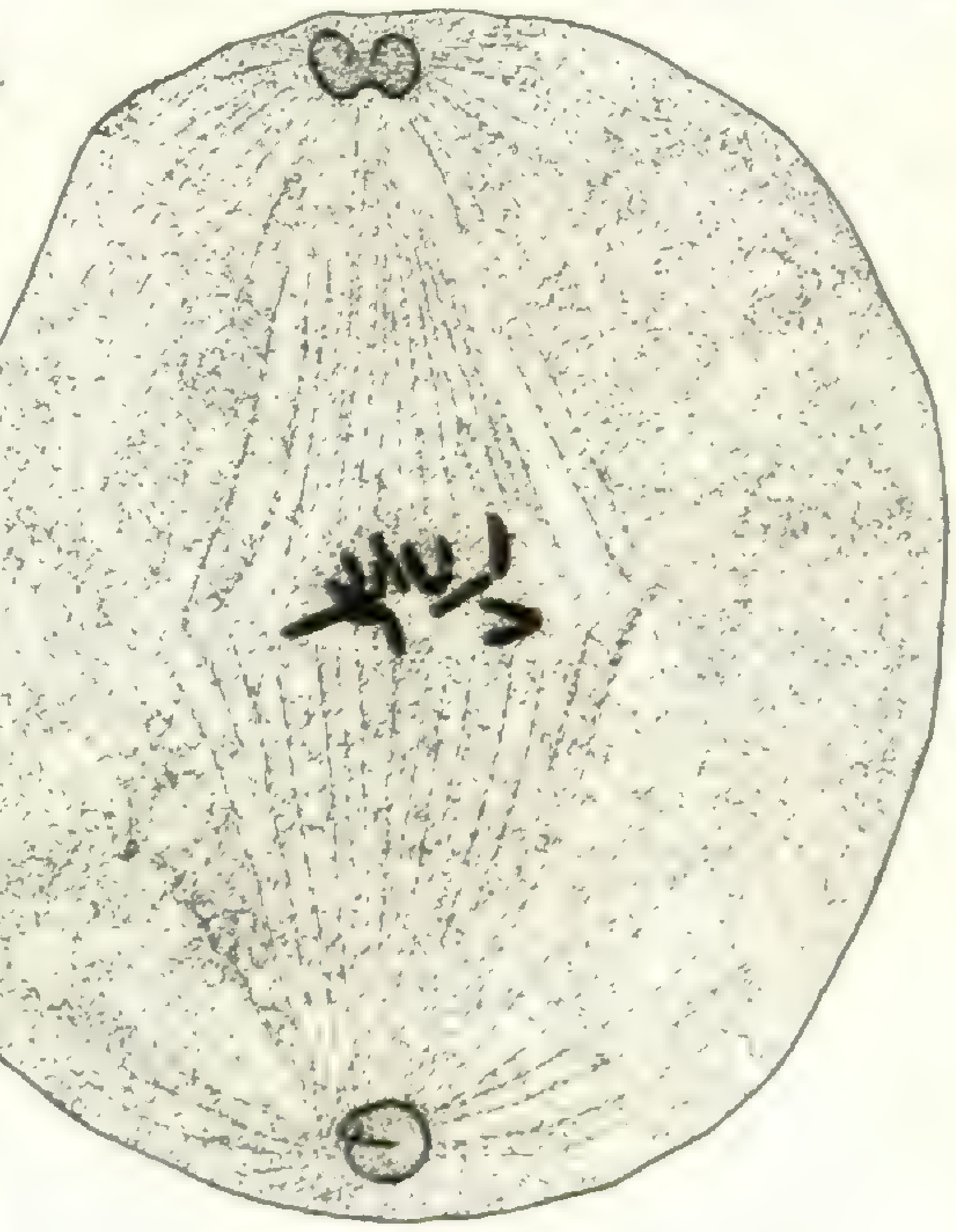

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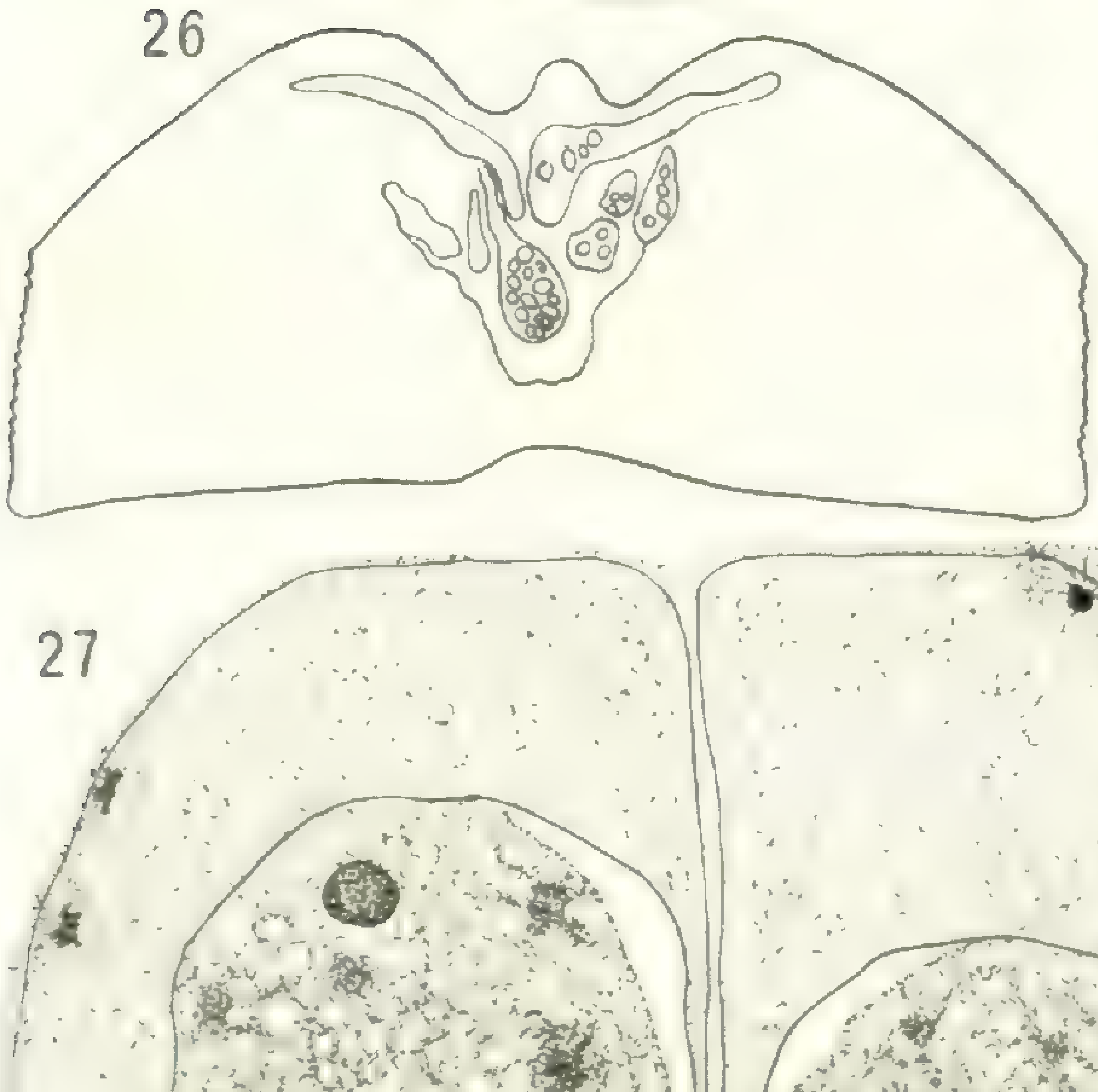

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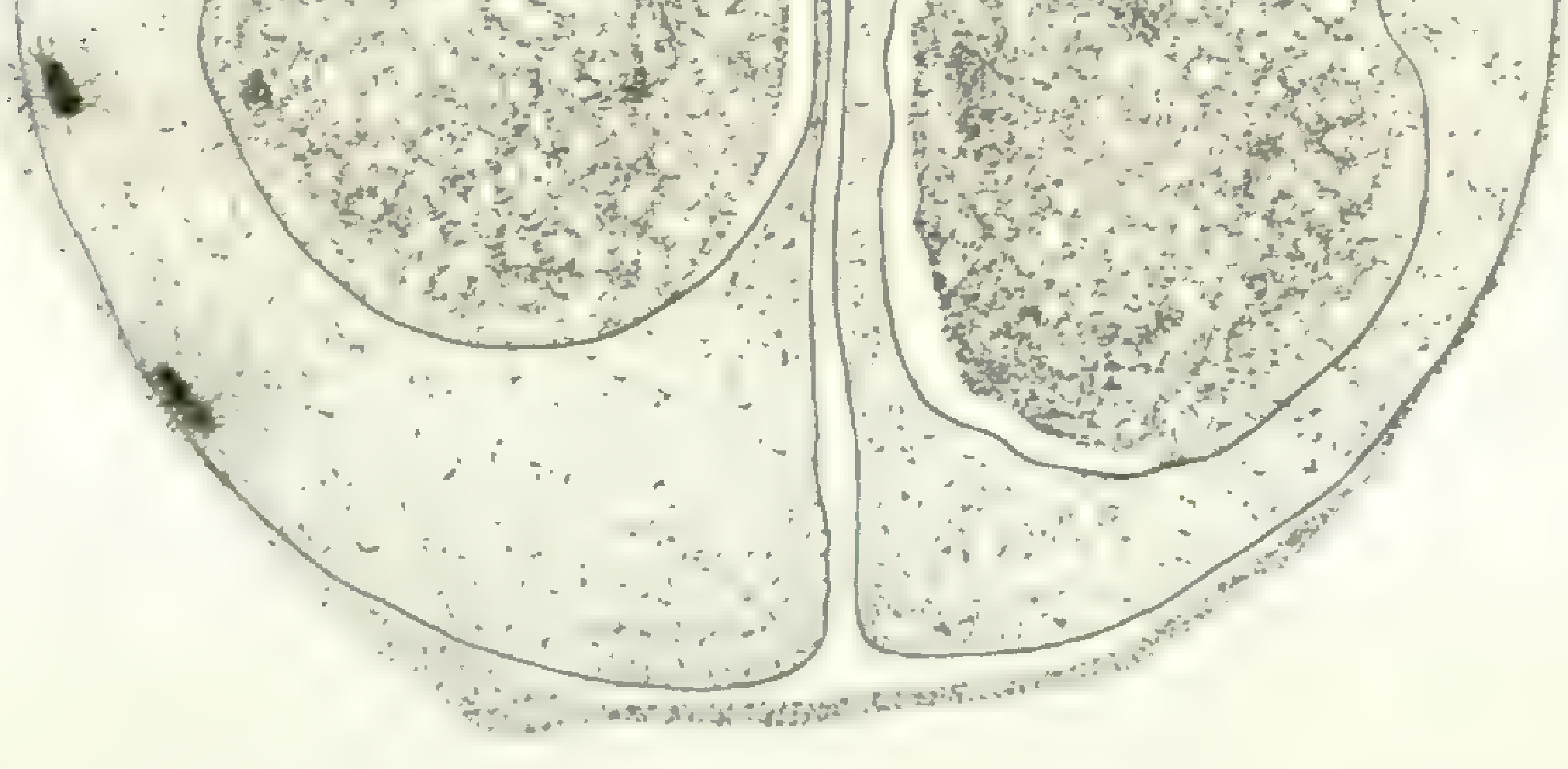

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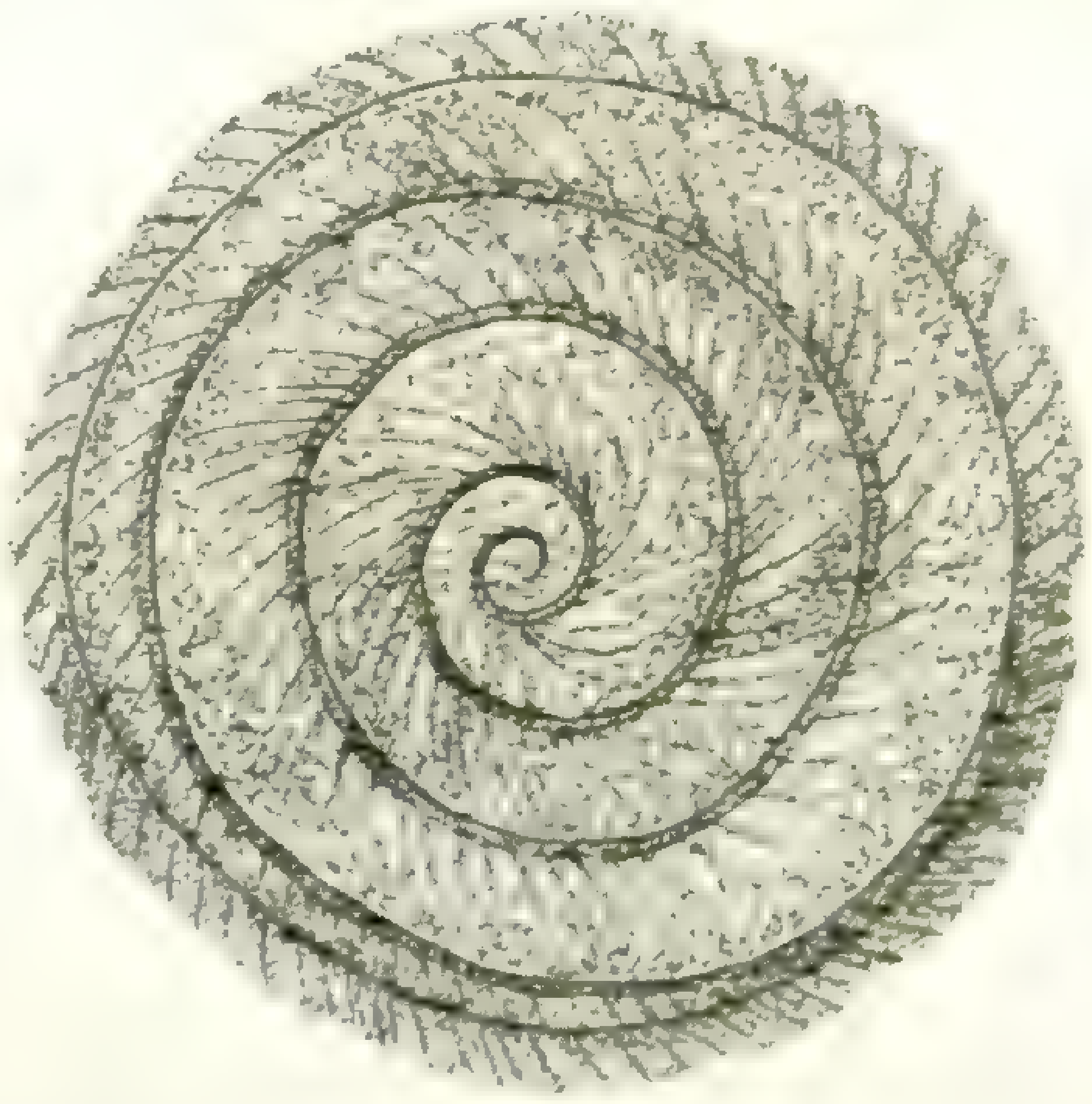

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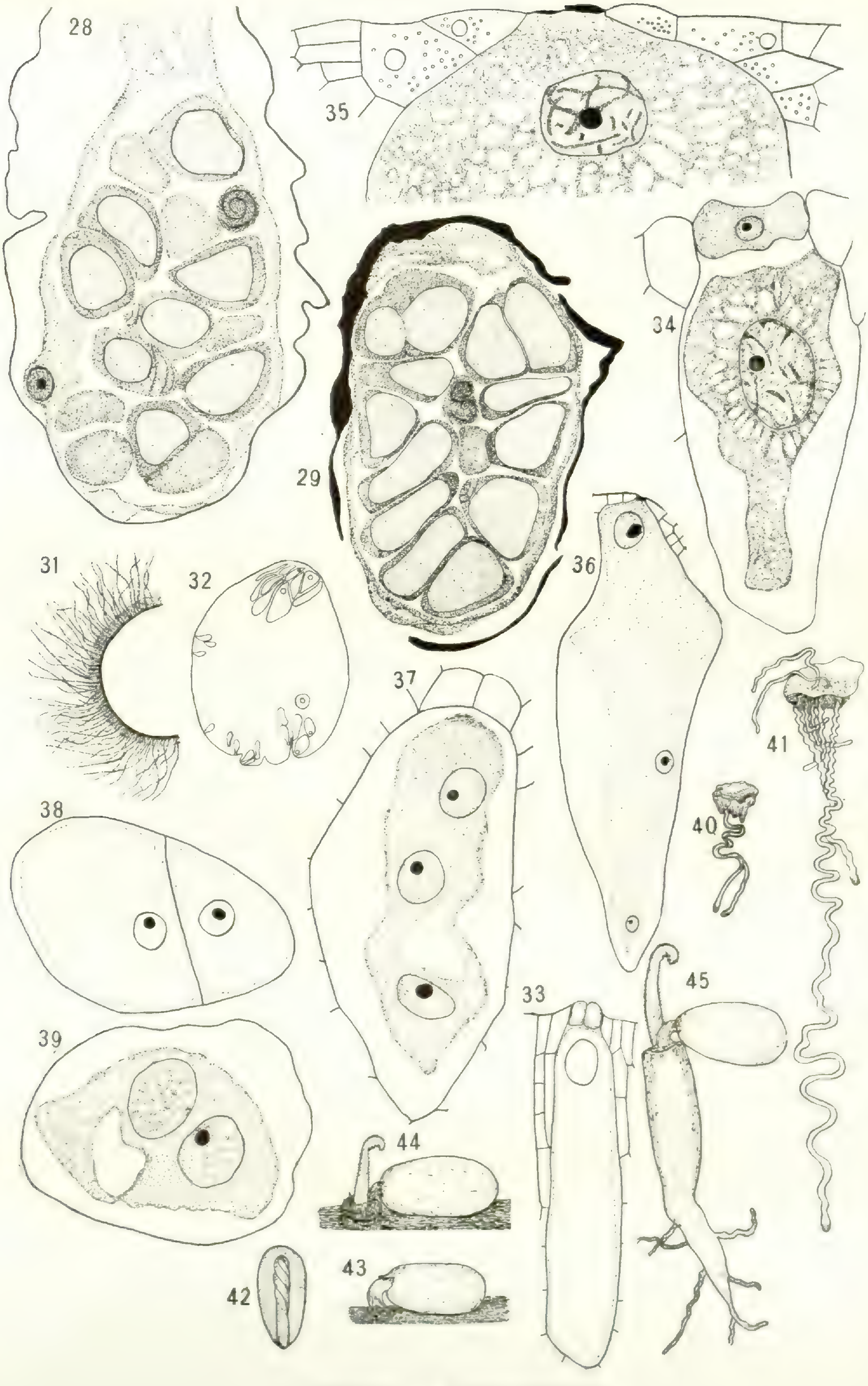
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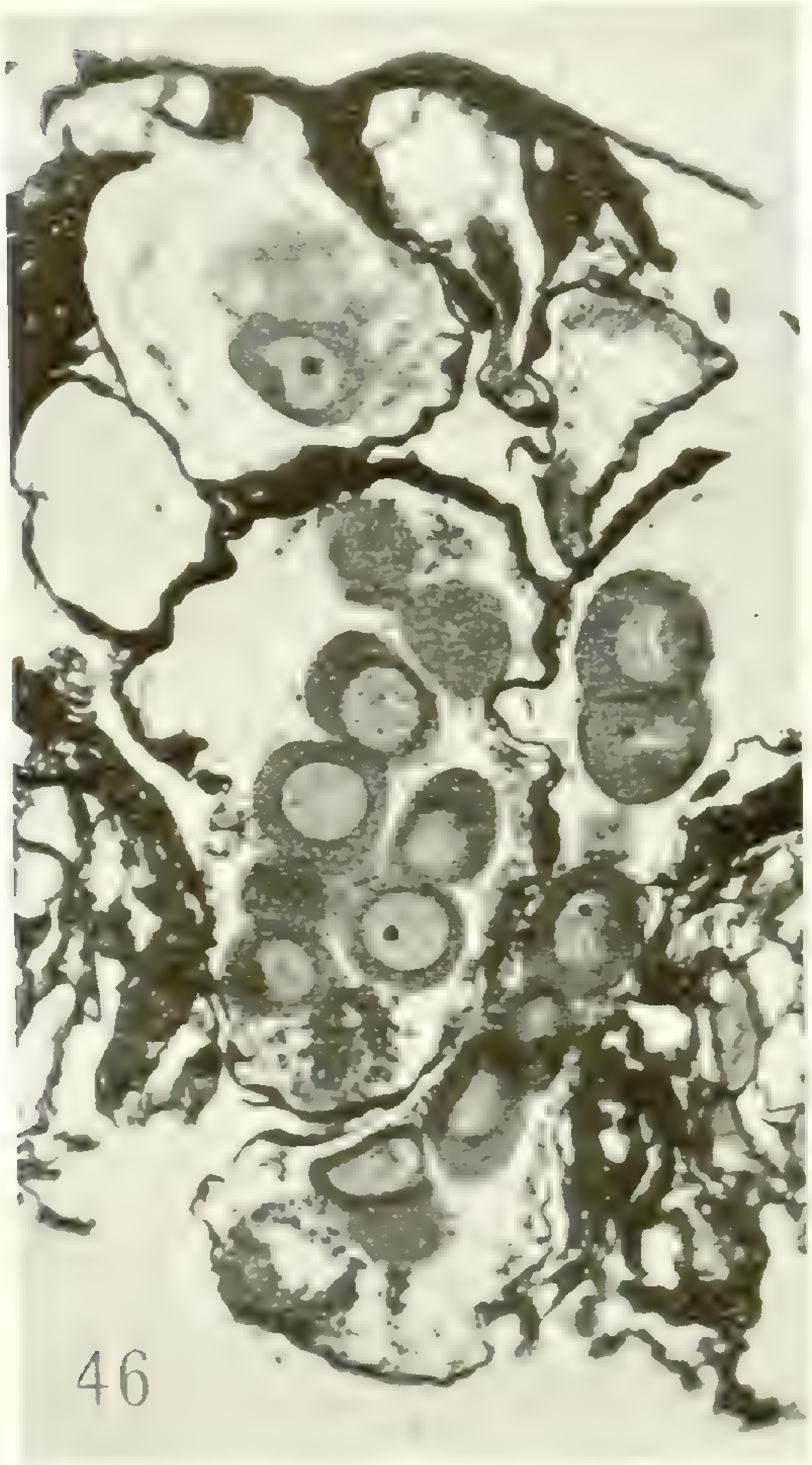
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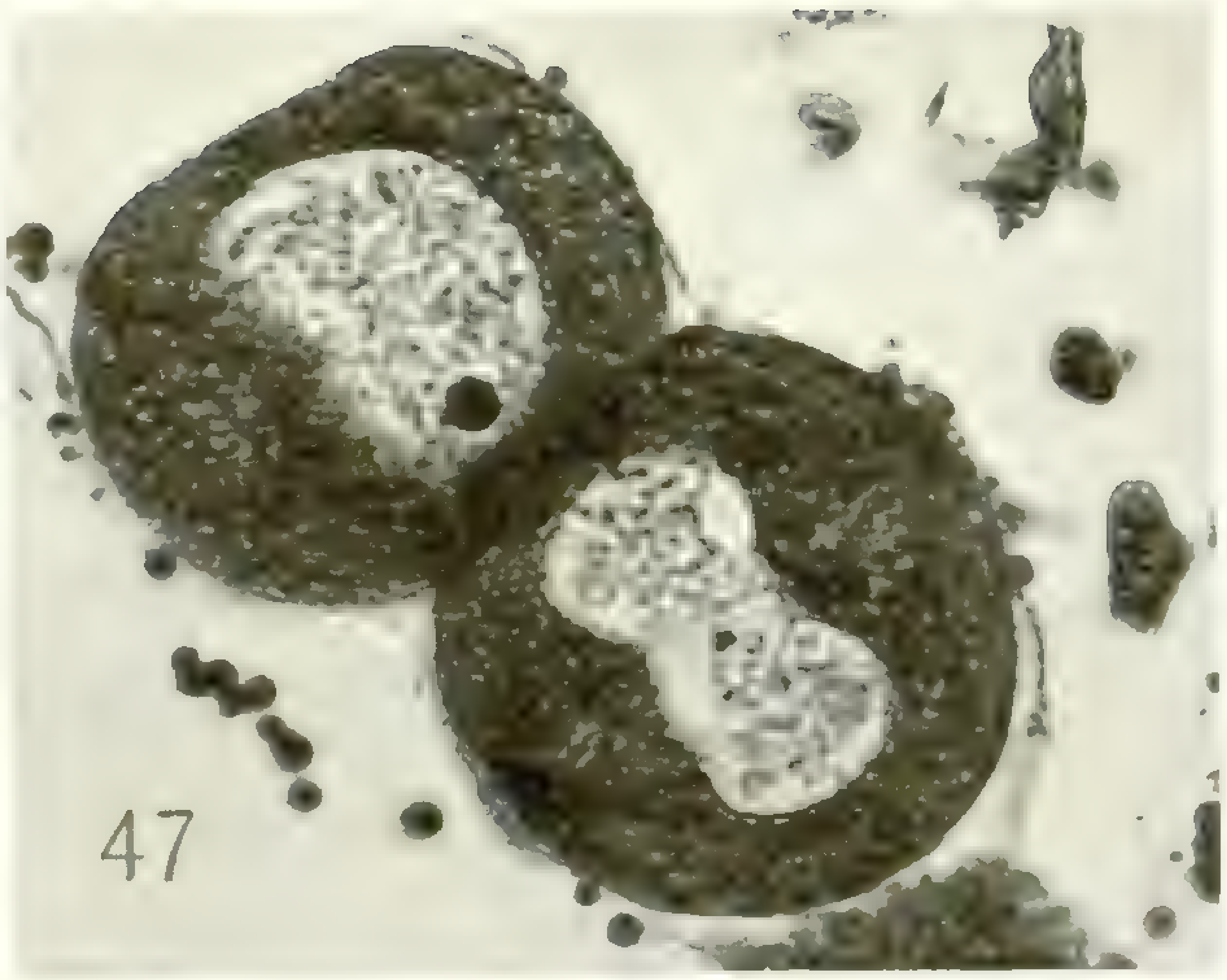
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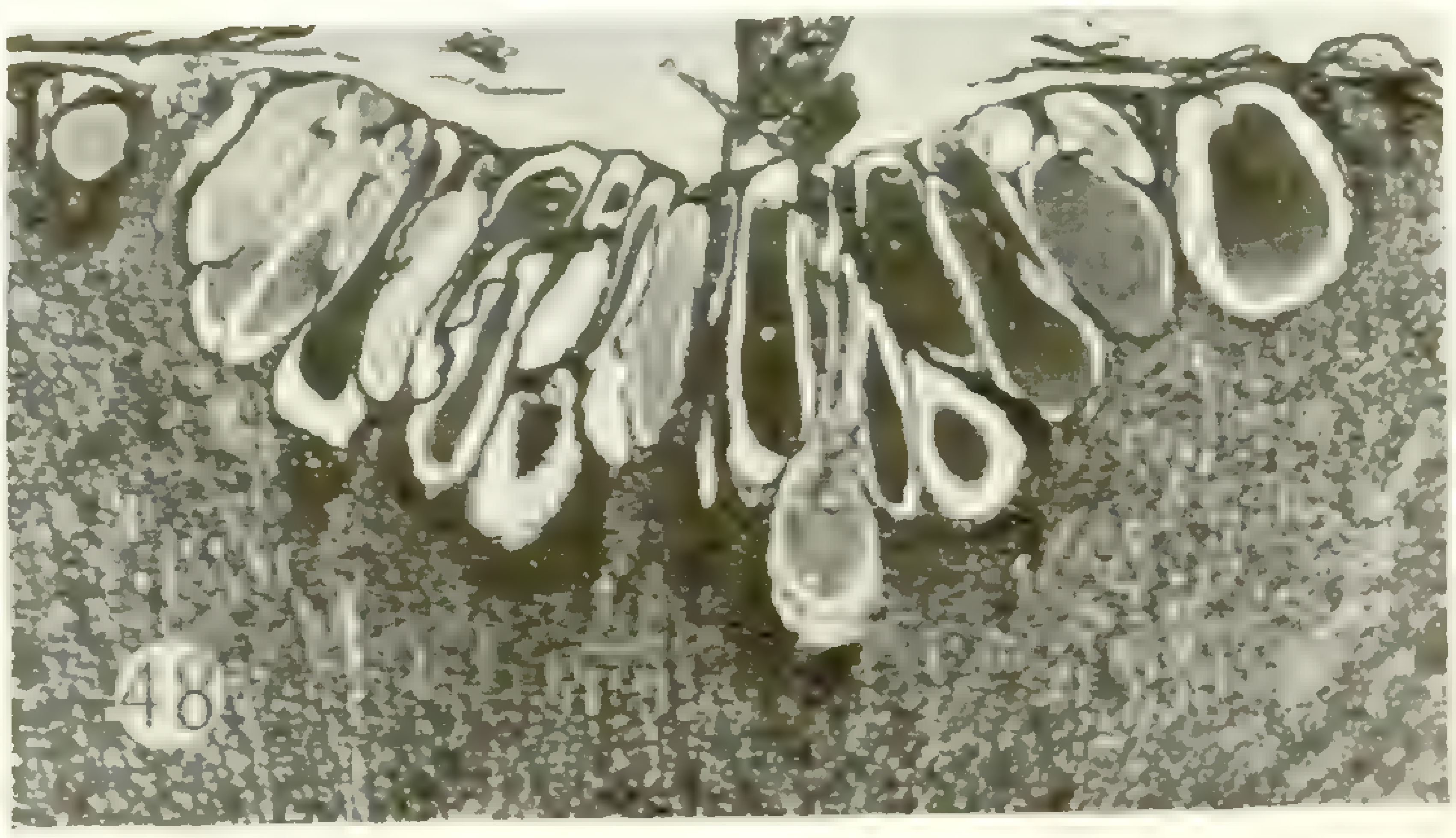
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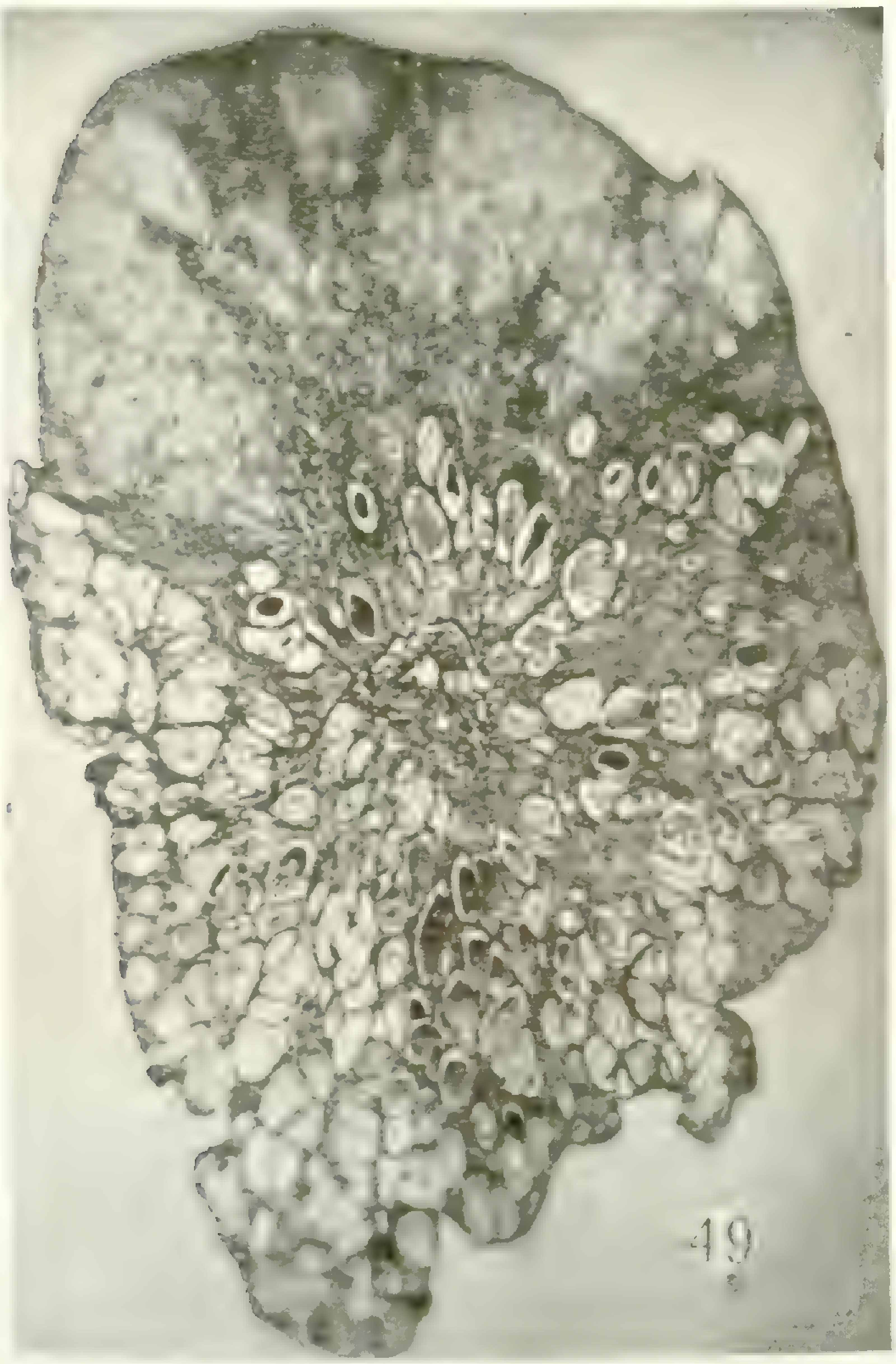
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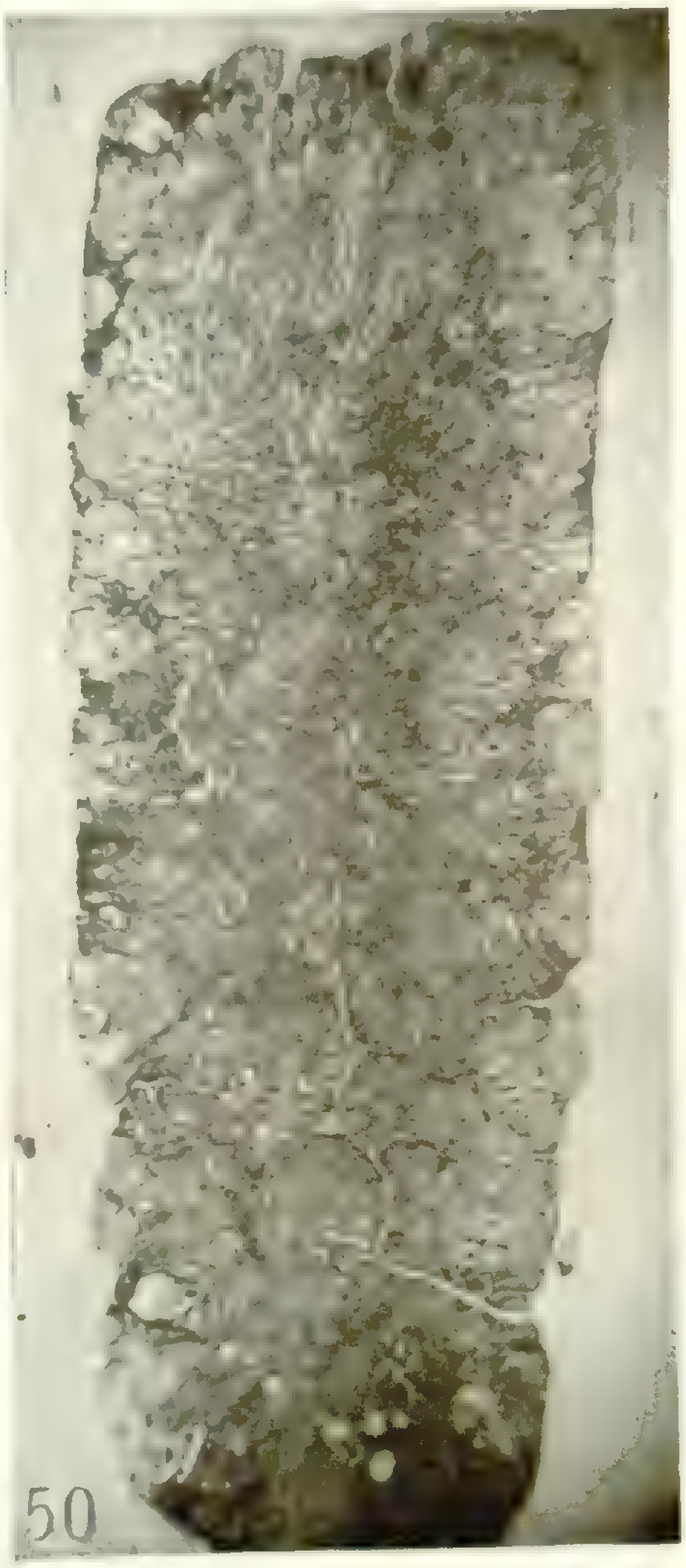
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CALDWELL on MICROCYCAS

apparently are beginnings of bud scales; first leaf circinate, distinctly hairy, and showing the beginning of leaflets. ×½.

FIG. 45. Plantlet, of same age as in *fig. 44*, removed from the earth; does not show scale-like growths. ×½.

PLATE XIII

FIG. 46. Pollen tubes in nucellus; body cells (eight in each of two tubes) seen in the ascending haustorial branches.

FIG. 47. Two body cells, showing form of nucleus, blepharoplasts, and radiating cytoplasm.

FIG. 48. Tip of female gametophyte, showing mass of archegonia.

FIG. 49. Cross-section of female gametophyte about 3^{cm} from micropylar end.

FIG. 50. Longitudinal section of female gametophyte, showing archegonia at micropylar end, along both sides, in median line, and at basal end.

APOGAMY IN NEPHRODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XCVIII

SHIGÉO YAMANOUCHI

This preliminary note will give a brief account of my cytological studies on apogamy in *Nephrodium molle* Desv., which were conducted at the Hull Botanical Laboratory, the University of Chicago, under the direction of Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN, to whom I acknowledge my great indebtedness for their suggestion and assistance in this investigation.

To undertake the solution of such an important problem as apogamy, it is absolutely necessary for an investigator to have beforehand a thorough knowledge of the nuclear condition in the normal life-history of a selected form. For this reason I have made a complete study of the normal life-history of Nephrodium in order to obtain the knowledge requisite for an investigation of the problem of apogamy.

The detailed account of this investigation, with plates and a discussion of literature, will be published later in three successive papers, entitled "Sporogenesis;" "Spermatogenesis, oogenesis, and fertilization;" and "A study of apogamy."

Mitoses in the sporophyte.—It was very easy to get the successive stages of the process of the vegetative mitoses in various parts of the leaf, but the most favorable figures were obtained during the formation of the sporogenous tissue.

The resting nucleus in the sporogenous tissue contains a delicate network with one or several nucleoli. Approaching the prophase of the mitosis the network passes into the continuous spirem, uniform in thickness and distributed throughout the nuclear cavity. Two kinoplasmic caps with few fibers are formed at the two poles outside the nucleus. The nuclear membrane becomes elongated a little toward the kinoplasmic caps and begins to break down at that point. Coincident with this the spirem segments into a number of chromosomes to which intruding spindle fibers become attached and finally establish an equatorial plate that has a characteristic aspect which will be shown in a final paper.

The chromosomes at the equatorial plate split longitudinally, and, after a peculiar change of their form, two groups of daughter chromosomes pass to the opposite poles of the spindle, where they become closely crowded in a mass. The polar view of this stage shows that the number of chromosomes is 128 or 132. Nucleoli fuse usually into one or two globules which decrease in size, finally vanishing during the prophase. The daughter chromosomes, crowded in a mass at the poles of the spindle, become so closely aggregated that it is hard to identify their individual outlines; then follows vacuolization of each chromosome.

The central spindle lying between two poles after organization of the daughter nuclei seems to contribute material for the formation of the cell plate, and consequently it proceeds from the center toward the periphery of the cell.

The resting nucleus of the spore mother cell contains a fine network of linin, in which the chromatin material is distributed in larger and smaller knots. With the further growth of the nucleus, the knots in the network decrease in size, whereas the delicate linin part increases in thickness, and finally there is formed a well-developed spirem, uniform in thickness and very much tangled. This state soon passes into the synaptic stage, which seems to culminate by location of the tangled spirem at one side of the nuclear cavity. The spirem consists of two threads, close together; in some parts the two are in contact side by side, and in the other parts they are fused into a single thread. These two threads may represent, according to the recent interpretation of synapsis, chromatin of maternal and paternal origin.

After synapsis, the tangled thread begins to uncoil and becomes distributed throughout the nuclear cavity; the spirem shows longitudinal splitting, but the two elements of the spirem which resulted therefrom remain closely associated so as to form a double thread, which finally segments into 66 or 64 chromosomes, each showing clearly its bivalent nature.

Fibrillar structures which first appear at the periphery of the clear region closely surrounding the nucleus become more and more pronounced until they approach the nuclear membrane, and when the membrane breaks down the fibers enter into the nuclear cavity from several directions.

When the spindle becomes bipolar, the chromosomes at the equatorial plate are arranged regularly, so that the counting of their number is easily done from the polar view. These 64 or 66 bivalent chromosomes separate and two sets of daughter chromosomes, each 64 or 66, pass to the poles of the spindle, and daughter nuclei are formed by the vacuolization of chromosomes.

Granularization of cytoplasm now begins at the periphery of the equatorial plate and proceeds toward its center, and seems to replace entirely the central spindles, so that the spore mother cell is divided into two hemispheres by the equatorial zone of granular cytoplasm.

Except in the number of chromosomes, the second, the so-called homotypic mitosis, is essentially the same in Nephrodium as the typical mitosis of the vegetative cell; 64 or 66 chromosomes reappear at the prophase of the second mitosis, split longitudinally, and are distributed into spores.

Spermatogenesis.—The mitoses in the vegetative cells of prothallia are similar to those of the sporophyte. The number of chromosomes, however, in this case is 66 or 64. The account of the mitoses which take place from the cutting-off of an antheridial initial from the superficial cell of the prothallia to the formation of sperm grandmother cells will be omitted. The number of chromosomes is always 66 or 64.

The sperm grandmother cell is characterized by the first appearance of blepharoplasts. The blepharoplasts first appear as two small granules at opposite sides of the nucleus, near the periphery of the cell, which means that the origin of the blepharoplast in Nephrodium is cytoplasmic. The resting nucleus of the sperm grandmother cell passes through the prophase, metaphase, anaphase, and telophase, the number of chromosomes being 66 or 64, and the blepharoplasts are always present near the poles of the spindle. After telophase, each daughter cell of the sperm grandmother cell or the sperm mother cell contains a single blepharoplast.

When the cell plate is completed, a new body appears near the nucleus of the sperm mother cell, far apart from the blepharoplast. For the sake of convenience, we shall term this body, at present, the *Nebenkern.*

The blepharoplast in close contact with the nucleus increases in size and assumes gradually a coiled band shape, while the nucleus, after an interesting modification of chromatin material, becomes also a coiled structure. The cilia appear only on the outer surface of the blepharoplast. The *Nebenkern* remains attached at the posterior end of the mature sperm, with the remnant of cytoplasmic material.

Oogenesis and fertilization.—In the formation of an archegonial initial from a vegetative cell of the prothallium, 64 or 66 chromosomes are present. The mitoses which occur in the formation of the central cell, neck and ventral cells, and neck canal, ventral canal, and egg cells, have very interesting peculiarities which will be described in a later paper. The noteworthy thing is that the number of chromosomes is 64 or 66.

Sperms pass through the archegonial neck and reach the egg cell. Normally a single sperm succeeds in entering, through the cytoplasm, into the egg nucleus which is in the resting condition. Within the egg the sperm finally loses its individual outline.

The fertilized egg nucleus in the resting state passes into the prophase of the first segmentation division. The spirem is a homogeneous thread structure, uniform in thickness, and seems to be continuous. It segments into a number of chromosomes that become arranged in an equatorial plate. The chromosomes in the equatorial plate split longitudinally and two sets of daughter chromosomes separate and pass toward the poles of the spindle. The polar view of this set shows that the number of chromosomes is 128 or 132.

The further processes of segmentation divisions during the development of an embryo were traced out in order to make certain the number of chrosomomes, and 128 or 132 are always present.

Apogamy.—The prothallia which produce apogamous sporophytes do not seem to be different from those which form normal embryos, so long as they remain a single cell layer in thickness throughout. The morphological structure does not seem to show any peculiarity. Numerous antheridia are produced. Although the mitoses which give rise to sperm mother cells from a primary spermatogenous cell are different from those of a normal case, yet the motile sperms are developed.

The most important and peculiar feature of the prothallia in connection with apogamous growth is as follows: The successive cell divisions proceed in the cushion region as usual in a normal case, but no functional archegonium is formed. In a certain portion in or near the cushion region, a superficial cell divides perpendicular to the surface of prothallium, while cells below the surface divide in various directions. Thus a mass of peculiar structure, whose further development would result later in an independent sporophyte, is worked out directly by the continuous growth of the prothallium.

The nuclear conditions were traced through the critical stage, intermediate between gametophytic prothallia and sporophytic structure, to the independent sporophyte. The number of chromosomes remains unchanged, always being 64 or 66. There is no migration of a nucleus from a neighboring cell to effect fusion, as is reported in Lastrea.

Conclusions.—The nuclear condition of *Nephrodium molle* may be summarized as follows:

1. The nuclei of the prothallia contain 64 or 66 chromosomes, the reduced, gametophytic, or x number. The nuclei of the gametes contain the same number. The fusion nucleus in the fertilized egg presents 128 or 132 chromosomes, the unreduced, sporophytic, or $2x$ number, which keeps unchanged until it is reduced during sporogenesis. Consequently it follows in the normal life-history of Nephrodium that the gametophyte contains the x number of chromosomes and the sporophyte the $2x$ number, and that sporogenesis and fertilization are the periods which mark the initiation of the two distinct generations.

2. The nucleus of a prothallial cell with the x number of chromosomes (64 or 66) sometimes becomes directly the nucleus of a sporophyte, apogamously produced; so that the x number of chromosomes continues through the whole life-history in the apogamous sporophyte. This fact does not seem to affect the fundamental idea that the alternation of generations is marked by the difference in the number of chromosomes in the normal life-history; but is simply an abnormal case of secondary importance. Still it must be admitted that in the case of apogamy at least the number of chromosomes is not the only factor which determines the character of the sporophyte and gametophyte.

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CURRENT LITERATURE

BOOK REVIEWS

Plant breeding

PROFESSOR DEVRIES has contributed a most interesting volume[1] to the literature of plant breeding and its relations to the current theories of evolution. It is a compact and popular presentation of the recent wonderful development in methods of plant breeding, and a clear statement of the bearing of all this vast experimental work upon the author's theory of mutation. Of special interest to American readers are the description of the methods and the results obtained at the Swedish station at Svalöf under NILSSON, and the comments upon the work of BURBANK. The work of the former will come to many as a revelation, and the work of the latter will be better understood.

The material of the book is derived chiefly from a series of lectures given during two summers at the University of California and the University of Chicago. It is presented under a series of topics, each of which is complete in itself, but all of which contribute to the general purpose of the author, as expressed above. This accounts for a certain amount of repetition, but it is the kind of repetition that uses the same material to illustrate the various points of view involved in a great conception. It is difficult to give an adequate idea of the contents of such a book, for the principles become convincing only when illuminated by the details of experimental work.

The first topic, entitled "Evolution and mutation," is a general introductory definition of the mutual relations of evolution, natural selection, and mutation, relations that seem to be persistently misunderstood. Unit-characters, as the essential feature of mutation, are defined; and hybridization is shown to result, not in new unit-characters, which characterize mutation, but simply in a new combination of unit-characters. This position is supported, not only by the author's experiments, but by numerous cases in horticulture, by the constancy of wild species, by the behavior of characters in crosses, by the occurrence of clearly defined small species within the ordinary species of wild plants and agricultural crops. It is claimed that the slow change of one species into another has not been proved, and that the mass of present evidence points to the origin of species from other species by "sudden leaps," which are called mutations.

The second topic deals with "The discovery of the elementary species of agricultural plants by HJALMAR NILSSON," whose work the author evidently regards as of the deepest significance, not only in practical plant breeding, but chiefly in reference to evolutionary doctrine. To develop the importance of NILSSON's work clearly, the author considers the general topic in four sections. The first is a historical sketch of the "Different principles in the breeding of cereals," in which the contributions of LECOUTEUR, SHIRREFF, HALLETT, HAYS, and VON LOCHOW are considered. The first two worked upon the principle of a single initial selection and subsequent rapid multiplication without further selection, in this sense being the precursors of the Svalöf method. Then came the domination of HALLETT, whose principle was accepted by German breeders, and seems to govern them to this day. Its two essential features are the initial choice, and the slow and gradual improvement by selection. With great force the author shows that all depends upon initial choice, subsequent selections only serving to isolate the deviating types; and these "initial choices" were never numerous. It is significant that DARWIN's theory of natural selection, based inferentially upon artificial selection, was developed at a time when this so-called "German method" prevailed, and the emphasis was being laid upon the continuous selection rather than upon the initial choice. The second section describes "The Swedish Agricultural Experiment Station at Svalöf." It began with the German conception of plant breeding, but soon changed to its present ideas. The results have shown that ordinary cultivated varieties of cereals are not pure, but are mixtures of well-defined and very numerous types; that when there is so great a range of types for selection, there is only loss of time in gradual amelioration by so-called methodical selection or in hybridization to secure new varieties. The third section presents "The Svalöf method of producing improved races," being a detailed account of the method of selection developed by NILSSON and his staff. Elementary forms are distinguished by definite "marks" (botanical characters) that have been found to be associated with certain industrial qualities. The selection is made only once, and the form is found to be quite uniform and constant, with the exception of accidental hybrids, which, however, also yield constant and pure races after repeated selection. The high variability which is commonly attributed to the ordinary varieties of cereals consists only in the differences among the constituents of the mixtures. The fourth section is "A criticism of the principles of continuous selection," and is a most effective analysis of the bearing of NILSSON's work upon the question of the origin of species by natural selection or by mutation. According to the author, the idea of unit-characters has changed the whole point of view, and the theory of mutation is supported by the general occurrence of elementary species and their constancy, by a comparison of the value of fluctuating variability and mutability among cereals, and by the researches of NILSSON. He goes so far as to claim that "the victory of the theory of a saltatory origin of species can no longer be doubted."

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[1] DEVRIES, HUGO, Plant-breeding; comments on the experiments of Nilsson and Burbank. Pp. xiii+360. Chicago: The Open Court Publishing Co. 1907.

The third general topic is "On corn breeding," and it is most interesting to read the comments of a trained European plant breeder upon the methods of breeding used in connection with this dominant cereal of the United States. The real breeding of corn began about ten years ago, with the discovery of the principle of single-ear selection, started by HOPKINS of the University of Illinois. The main difference in the breeding of corn and other cereals is that among the latter cross-pollination is an exception, while with corn it is the rule, and repeated selection becomes necessary to eliminate the effects of previous crosses (not for slow improvement, as commonly supposed). One catches glimpses of the immense possibilities in breeding corn, as well as the amateurishness of our current methods.

The fourth topic is entitled "The production of horticultural novelties by Luther Burbank," who has the misfortune of being both overestimated and underestimated. No one is better equipped than DEVRIES, through training and temperament, to reach a true estimate, and hence this section of the volume is of great interest. The topic is presented under four divisions, the first dealing with "Methods and material." BURBANK is described as "a man who devotes his whole life and all his energies to the introduction and production of new, beautiful, and useful horticultural plants," and who has rediscovered many of the practices more or less universally known in Europe. A special feature of his work is the large scale on which his selections are made; and his main work consists in the production of new horticultural varieties by crossing, getting combinations of desirable qualities, and eliminating undesirable ones. The second section gives details of the conspicuous "New varieties of fruits and flowers" originated by BURBANK. There is an analysis of the simpler methods of producing what are called "new varieties" in horticulture, with illustrations from some of BURBANK's most notable achievements, so far as the author could get at the scientific side of his performances by questioning. The general conclusion to be drawn from his operations is that combinations of characters can be obtained by crosses in almost any arbitrarily chosen direction or degree, but that new unit-characters are probably never produced. The third section deals with "Hybridization and selection" as practiced by BURBANK. The aim of the hybridizer is to upset the constancy of his plants and produce an extreme chaos of forms, from which his selections may be made. To get the real pedigree of any plant in this chaos is impossible, and the hybridizer does not care, for he is only after the results. BURBANK is credited with "a special gift of judgment" in his selections, but his results are new combinations of characters and not the production of new characters. All such practical hybridizing and selection "afford highly valuable resources for theoretical discussion, but on single points they should not be accepted as definite proofs, but only as indications for more circumscribed experiments." The last section, entitled "Mutations in horticulture," shows that most new horticultural varieties originate as "chance seedlings," many illustrations from BURBANK's work being used to show that it is the occasional "chance plant" with some peculiar character that has been seized upon and propagated. It would seem, therefore, that mutations in horticulture have been frequent.

The very important fifth topic is "The association of characters in plant breeding," and it is presented in five sections. The first discusses "Association of characters in nature," and shows that there is a regular coincidence of marks hitherto regarded as independent of one another, as the association of the color and hairs of the leaves of the seedlings of common stock with double flowers; of the characters of the foliage of the quince with the qualities of the fruit; of the form and hairiness of the scales of barley with the practical qualities of the grain. The author believes that a discovery of the laws governing such "correlations" may give us a certain amount of power over them that will prove of immense practical and experimental importance. The second section illustrates "Correlations in agricultural breeding," and it is stated that "to the practical breeder it shows the way in nearly all the burning questions, and for the scientist it may give the solution of numerous problems which have eluded his evolutionary speculations for more than half a century." The third section, entitled "A methodical study of correlations," describes in detail the remarkable system of records developed at Svalöf to keep track of all the marks and their associations. It is called "a model of the combination of science and practice." The fourth section deals with "Correlations in fluctuating variability," and is a theoretical discussion of the influence of external life-conditions on the phenomena of correlation, illustrations being taken from teratology and from agricultural plants. The cause of this parallelism between different organs is seen in nutritive factors most prominently, minor ones being temperature, moisture, light, etc.; and illustrations are given to show how such factors would affect several regions simultaneously. The last section deals with "Unit-characters," and is a most fundamental speculation from the standpoint of evolution. Each organism is conceived of as a "microcosm, consisting of thousands of elementary entities, which combine to give it its form and function." These are the units which govern and control the visible characters and qualities. The larger the number of common units and the smaller the number of different units, the greater will be the affinity. As to the nature of a "unit," there are two points of view. They may be approached by analyzing the visible characters and reducing them to independent groups; or there may be some invisible, although material cause, which constitutes the real source of each unit. There is no reason to assume that a unit should be limited to one organ, to one tissue, or to one cell. A unit may show its activity in different organs, sometimes even in almost all parts of a plant. This explains correlations and "has overwhelming importance in hybridism." Crosses give insight into the nature of unit-characters, showing what marks belong together, and dividing so-called characters into their constituent units. When one unit is added to or subtracted from a well-known type, the result is a mutation. The author is impressed with the idea that the study of correlations must be conducted on the broadest possible lines, and that in this direction we shall approach some definite knowledge of evolution.

The last topic is "The geographical distribution of plants" and is chiefly an expression of doubt as to the real value of the current ideas concerning the nature of adaptations of organisms to their environment. For example, the current view of desert plants is that they are "astonishingly specialized and adapted for large regions where it is impossible for other plants to thrive." It is a natural inquiry, however, whether all these species are natives of the desert and have acquired their special characters under the influence of their environment. "Is it the desert which has made them what they are, or are they perhaps only a selected few from among the widely differentiated forms which are everywhere abundant on more favorable soils?" Present distribution is the result of migration, and migration is directed by the given characters of the species. The qualities of organisms are the causes, and the distribution is the result.

Altogether, the book is full of pregnant suggestions, and should do much toward clearing up some of the evident confusion concerning the views of the distinguished author.—J. M. C.

Progressus Rei Botanicae

Genetics.—In the valuable series of botanical reviews published by the Association Internationale des Botanistes under the title *Progressus rei botanicae*, BATESON[2] traces the progress made in the study of heredity by the pedigree-method since the rediscovery of MENDEL'S principles. For this discipline, which has so rapidly advanced to a place of prominence among the biological sciences, he proposes the name *genetics*.

The expressed object of the author, "to give an account of the progress in the study of heredity and variation which has followed the rediscovery of MENDEL'S work," has been carried out in a full and complete way, except for the notable omission of all but a passing reference to biometrical work, which has also made good progress during the same period, and which also belongs, at least in large measure, in the field of genetics. This omission is evidently due to the desire on the part of the author to avoid everything of a controversial nature. The literature of Mendelian heredity is fully cited and discussed, and the bibliography appended includes 140 titles. Certainly no one could have been selected to present the side of genetics represented by Mendelian hybridization, who is in position to speak with more authority than BATESON, and this summary of the literature to the early months of 1906 is of great value to all interested in the general subject.—G. H. SHULL.

Immunity.—As an introduction to this part, by R. P. VAN CALCAR,[2] the fundamental principles of adaptability of plasmodia to rising concentrations of glucose and the general influence of chemotaxis are discussed. The reactions to toxic ferments by the cells of some plants, in consequence of which the cell walls increase in thickness, are considered in the sense of self-defense or immunity. Similar protective processes are described in reference to bacteria. From these general considerations the author proceeds to the more complex subject of immunity in the animal body. After briefly explaining the theory of phagocytosis of METCHNIKOFF, the immensely important work on hemolysis is given its proper place as opening up new fields of research in immunity. The specificity of the phenomena accompanying the formation of agglutinins and precipitins is brought to the attention of the reader, and their diagnostic value is discussed *pro* and *con*. The crowning theory of immunity, EHRLICH'S side-chain theory, is then taken up at some length and its points of contact with METCHNIKOFF'S theory brought to light.

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[2] BATESON, W., The progress of genetics since the rediscovery of Mendel's papers. Progressus rei botanicae 1:368–418. *figs. 24.* VAN CALCAR, R. P., Die Fortschritte der Immunetäts- und Specifitäts-Lehre seit 1870. *Idem*, pp. 533–642 *figs* 20. Jena: Gustav Fischer. 1907. *M.* 18 the volume.

The difficult task of discussing the important subject of immunity has been ably executed and a large amount of information is given in this book. The author has done justice to the various workers who have contributed to the development of modern views, and has striven to bring into harmony to some extent the opposing opinions of different factions. The subject is much condensed, in some instances almost too much so, yet without seriously interfering with clearness and conciseness. The volume is admirably suited for those students who wish to obtain a general insight into the subject without going into detail. A complete list of the literature enables the student to investigate any particular subject he may be interested in.—P. G. HEINEMANN.

MINOR NOTICES

North American Uredineae.—In Part III of the first volume of this work, HOLWAY[3] continues his presentation of Puccinia in the order of hosts, concluding Leguminosae and extending through Halorrhagidaceae. The species numbers extend from 84 to 120, including three new species on Sidalcea, Viola, and Boisduvalia. The clear text and the excellent plates reproducing photomicrographs of the spores make this monograph most attractive in appearance.—J. M. C.

Acta Horti Bergiani.—The fourth volume of this series,[4] under the editorship of WITTROCK, is dedicated to the bicentenary of LINNAEUS. It contains seven papers, illustrated by 24 plates, many of them handsomely colored, and 176 text figures, and deals chiefly with forms under cultivation in the Bergian garden. VEIT B. WITTROCK (pp. 32) gives an account of the life and work of LINNAEUS, illustrated by three portraits. H. DAHLSTEDT (pp. 32. *pls. 2. figs. 8*) gives an account of seven new species of Taraxacum under cultivation. NILS SYLVEN (pp. 8. *pl. 1*) describes two Senecio hybrids. S. ALMQUIST (pp. 88. *pl. 1. figs. 84*) describes numerous forms of Rosa, many of them called mutations. GUST. O. A:N MALME (pp. 16. *pls. 4*) describes forms of *Victoria cruziana*. ERNST ALMQUIST (pp. 92. *figs. 66*) describes and illustrates a surprising number of elementary species of *Capsella Bursa-pastoris*. VEIT B. WITTROCK (pp. 187. *pls. 13. figs. 18*) shows that *Linnaea borealis* is an exceedingly polymorphic and polychromic species, the latter fact appealing strikingly to the eye in the eight handsomely colored double plates, nearly 150 new forms being described.—J. M. C.

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[3] HOLWAY, E. W. D., North American Uredineae. Vol. I, Part III. *pls. 24–36*. Minneapolis, Minn. 1907.

[4] Kungl. Svenska Vetenskaps-Akademiens Trädgård Bergielund. Stockholm. 1907.

NOTES FOR STUDENTS

Recent anatomical papers.—A very detailed account of the leaf structure of American Lauraceae has been given by PETZOLD,[5] his purpose having been to establish at least generic anatomical characters. The leaf structure, however, proves to be quite uniform, and generic distinctions are not feasible. For example, a concentric structure is characteristic of Silvia, but occurs also in a few species of Phoebe and Nectandra; a hypoderm is developed in Cryptocarya and Hufelandia, but also in some species of Ocotea, Persea, and other genera; a closed sheath of stereome surrounds the veins constantly in some genera, but not in others; crystals of calcium oxalate, otherwise so frequent in this family, do not occur in Lindera and Dicypellium, but they are also absent in several species of other genera. The paper is a welcome contribution to the knowledge of the anatomy of these plants, even if no generic characterization seems possible.

The structure of leaves, seeds, and pollen of Polemoniaceae have been examined by HÜLLER,[6] his material including a large number of American species. It deserves mention that calcium oxalate was detected in certain species of Collomia and Gilia as single crystals, and as druids in the monotypic Bonplandia. The stomata were always observed to lack subsidiary cells, thus agreeing with the type of Ranunculaceae. Trichomes as covering-hairs and as glandular hairs are very common, representing several characteristic forms. In the midrib of *Phlox Drummondii* and various species of Gilia, the mestome strand contains two or sometimes several groups of leptome.

In regard to the structure of the seed coat, Phlox is the only genus in which the epidermis contains mucilage only in the outer wall beneath the cuticle. The peculiar spirals of cellulose were noticed in most species of all genera except Phlox. Inside the epidermis there are usually some strata of compressed tissue and a pigment layer; but in Cobaea a fourth tissue was absent, namely, woody parenchyma beneath the epidermis. The nutritive tissue, which is relatively sparingly developed, contains oil and aleurone.

The pollen grains are globose or elliptic, and the exine is never smooth, but covered with protuberances in the shape of ridges or granules in numberless variations. There are always more than three germ-pores, from four to many, and in some cases scattered irregularly over the surface. Although the author had to depend upon dried specimens, the results are nevertheless quite interesting and of importance to systematic anatomy. However, a study of fresh material, including the stem and root, would be highly desirable.

Forty-three species of Meliosma (Sabiaceae) have been examined by DIHM.[7] The palisade tissue is very characteristic in representing a modification of HABERLANDT'S "arm palisade parenchyma," differing from it in the several arms or branches being borne upon a larger basal cell. This peculiar modification is called by the author "coralloid palisade parenchyma," and is known only in Meliosma. The pneumatic tissue is often very open and passes insensibly into the palisade tissue; and it appears as if the chlorenchmya might be composed merely of pneumatic tissue modified somewhat on the upper face of the leaf-blade. Calcium oxalate occurs in all the species of Meliosma, and mostly as druids; globose conglomerations, however, were also observed in some few species.—THEO. HOLM.

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[5] PETZOLD, V., Systematisch-anatomische Untersuchungen über die Laubblätter der amerikanischen Lauraceen. Bot. Jahrb. **38**:445–474. 1907.

[6] HÜLLER, G., Beiträge zur vergleichenden Anatomie der Polemoniaceen. Beih. Bot. Centralbl. **21**^{1}:173–244. *pl. 8 figs. 25.* 1907.

[7] DIHM, H., Das Blatt der Gattung Meliosma in anatomischer Hinsicht. Beih. Bot. Centralbl. **21**^{1}:117–147. *pls. 5–6. figs. 21.* 1907.

Origin of the yeasts.—The problem of the autonomy of the group of Saccharomyces has been reopened by the researches of VIALA and PACOTTET.[8] In two ascomycetes, *Gloeosporium ampelophagum*, the anthracnose of the grape, and *G. nervisequum*, the anthracnose of the plane-tree, they have found a complex polymorphism, the most striking feature of which is the presence of conidia capable of budding in yeast-like fashion and of forming endospores in cysts, like yeasts, but which are produced from the true ascomycete mycelium. Other fungi, such as the Mucorineae, Ustilagineae, etc., bud in this fashion also, but the formation of endospores was regarded by HANSEN as a certain characteristic of true yeasts. If these observations of VIALA and PACOTTET are correct, they would seem to indicate that what are known as yeasts may only be forms of polymorphic ascomycetes.

GUILLIERMOND,[9] in reviewing this work, grants that there may be such forms, but strongly suspects that the cultures were impure and contained not only the Gloeosporium but also a yeast living with it. The most experienced observers have been led into errors from this same cause. In defense of the autonomy of the Saccharomycetes and at the same time of the interpretation of the cyst producing endospores as an ascus, GUILLIERMOND[10] gives a general review of the yeast situation. The extended work of HANSEN and his students has made it highly improbable that our industrial yeasts could ever revert to the mycelial condition, that is, their characters have become so fixed that now they form an independent and distinct group of the ascomycetes. The conjugations in such yeasts as *Zygosaccharomyces Barkeri* and *Schizosaccharomyces octosporus*, as they have been observed by BARKER[11] and GUILLIERMOND, is the strongest reason for considering the resulting product as an ascus. This conjugation, with its fusion of nuclei and subsequent division into endospores, is regarded by GUILLIERMOND as the equivalent of the fusion of the two nuclei in the ascus and the formation of ascospores. It is true that a majority of the yeasts do not show this conjugation, but this may be due to the fact that they have become parthenogenetic. The conjugation observed in *Saccharomycodes Ludwigii* by GUILLIERMOND, where the endospores conjugate before germination, may be only a secondary development introduced into parthenogenetic forms as a means of recuperation. "The existence of the conjugation preceding sporulation, coupled with the cytological character of the sporange, demonstrate in an evident manner the ascogenous nature of this organ, and one ought to consider with HANSEN that the Saccharomyces constitute an autonomous group belonging to the Ascomycetes and near to the Exoascaceae."—B. F. LUTMAN.

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[8] VIALA et PACOTTET, Compt. Rend. Acad. Sci. Paris **142**:458–461. 1906.

[9] GUILLIERMOND, A., A propos de l'origine des levures. Ann. Mycol. **5**:49–69. 1907.

[10] GUILLIERMOND, A., Rev. Gén. Bot. **17**:337–376 *pls 6–9* 1905.

[11] BARKER, Phil. Trans. Roy. Soc. London B. **194**:467–485. *pl. 46.* 1901.

Heredity in micro-organisms.—Working with the yeast *Saccharomyces anomalus* and the bacteria *B. coli-communis*, *B. typhosus*, and *B. megatherium*, BARBER[12] has extended the investigations of HANSON, BEIJERINCK, CONN, MAYER, and others on such variation as may arise spontaneously from cells which vary independently of environment. The cells chosen were those showing a morphological difference from the parent, and the new races of descendants were tested further for biochemical differences. The problem of isolation was thus a much more difficult one than that of selection of bacterial "sports" in mass with physiological differences, such as that of a white colony among red pigmented ones. BARBER devised and describes an ingenious method for isolating single varying cells from a hanging drop under the microscope by means of a capillary tube, with apparatus for holding and adjusting it under the lens. A single cell drawn into this could be discharged into another hanging drop, placed in a sealed moist chamber, and its development and descendants watched for as many generations as necessary. With the yeast BARBER obtained in this way new races whose morphological characters (large, long cells) persisted over three years, such a new race successfully competing with the parent stock when mixed with it in culture. Attempts to further modify the race by selection failed. Much the same results were obtained with the bacteria. These varieties were true mutations, appearing suddenly with full-fledged characters, apparently independent of natural selection and comparable with sports among multicellular organisms. If physiological characters are correlated with morphological, as in the case of increased power of fermentation of one of BARBER'S races of *B. coli*, it seems probable that mutation may be a factor in the origin of increased virulence of some pathogenic bacteria.—MARY HEFFERAN.

Position of the nucleus.—KÜSTER[13] has made a rather extensive series of observations upon the relation between the position of the nucleus and cell growth and the formation of membranes. His conclusions differ from those of HABERLANDT, especially in reference to the position of the nucleus in root hairs and stomatal apparatus, and in cells undergoing local thickenings of the cell wall.

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[12] BARBER, MARSHALL A., On heredity in certain micro-organisms. Kansas Univ. Sci. Bull. **4**:3–48. *pls. 1–4.* 1907.

[13] KÜSTER, ERNST, Ueber die Beziehungen der Lage der Zellkernes zu Zellenwachstum und Membranbildung. Flora **97**:1–23. 1907.

While KÜSTER confirms HABERLANDT'S observations that the nucleus is usually near the tip of the rhizoid in many plants, he finds that in *Hydrocharis morsus-ranae*, and in many other plants of similar habitat, the nucleus is just as constantly at the base of the root hair. The suggestion is made that the position of the nucleus in root hairs may be a result of growth rather than a cause of it, or the position may be due to unknown factors.

In regard to the position of nuclei in the stomatal apparatus, KÜSTER is inclined to believe that the position of the nuclei of the neighboring cells is not related to the development of the guard cells, but rather that the position near the concave wall is due to physical factors which favor or compel this position. In many plants, like *Osmunda regalis*, when the neighboring cells are not crescent-shaped, the nuclei are not situated near the walls.

Although KÜSTER agrees with HABERLANDT that the nucleus is often found at the place where local thickenings of the cell wall are taking place, he also finds other instances where the nucleus is not so situated.

In these three classes of phenomena, KÜSTER regards HABERLANDT'S explanations as teleological. He himself, however, is not able to find a satisfactory explanation for the varying position of nuclei and he believes that the factors which determine it have not yet been discovered.—CHARLES J. CHAMBERLAIN.

Items of taxonomic interest.—J. N. ROSE (Smithson. Quarterly 50:32. 1907) has made additions to his synopsis of the Mexican species of Ribes and has described a new species; has proposed, in connection with J. H. PAINTER (*idem* 33–34), the new generic name *Morkillia* for *Chitonia* Moç. and Sessé (Zygophyllaceae), which is a homonym of *Chitonia* D. Don.; and has described (*idem* 63–64. *pl. 6*) a new Cactus from Guatemala, a species of the Melocactus type, to which he proposes to shift the generic name Cactus.—N. PATOUILLARD (Bull. Soc. Mycol. France 23:50–52. 1907) has described a new genus (*Le Ratia*) of hymenogasters from New Caledonia.—H. HARMS (Bot. Jahrb. 40:15–44. 1907), in his fourth paper on African Leguminosae, has described a new genus, *Englerodendron*.—R. HAMET (Bull. Soc. Bot. France 54:26–38, 52–76. *pl. 2*. 1907) has published a synopsis of the genus Drosera, recognizing 65 species, setting aside 4 as insufficiently known, and excluding 7.—S. BROWN (Torreya 7:125, 126. 1907) has described a new spruce (*Picea albertiana*) from the Canadian Rocky Mts., which had been referred to both *P. canadensis* and *P. mariana*.—A. ZAHLBRUCKNER (Ann. K. K. Naturh. Hofmus. 20:350. 1907), in centuries xii and xiii of his *Kryptogamae exsiccatae*, publishes a new lichen (*Rinodina iowensis*) from granite rocks near Fayette, Iowa.—J. M. C.

Vegetation in Somerset, England.—Following the lead of the late ROBERT SMITH, vegetation maps are multiplying in England. The latest is that of the Bath and Bridgewater district of Somerset, and is the work of C. E. MOSS.[14]

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[14] MOSS, C. E., Geographical distribution of vegetation in Somerset: Bath and Bridgewater District. Publ. Roy. Geog. Soc. London. pp. 71. *figs. 24. colored map.* 1907.

The lowlands area is presented under the following formations: dune, muddy salt marsh, rocky headlands, aquatic, and peat moor. The section given to a consideration of the upland area contains an account of the plant formations of the sandstones, the limestones, the deep marls and clays, and the region of cultivation. The history of the plant formations is traced, it being shown that a plant formation begins as an open or unstable association, passes through intermediate associations, and eventually becomes a closed or stable association. For example, the dune formation in this region begins as an open association, either of strand plants, or of *Agropyron junceum*, or of *Ammophila arundinacea*, and only reaches the intermediate associations of dune pasture plants or of dune marsh plants. The formation of the muddy salt marshes begins as an open association of Salicornia, and, after reaching an intermediate association of halophilous plants, the salt marshes are reclaimed. The author concludes that in a small area, like England, the plant associations are determined much more by edaphic factors than by climatic conditions.—J. M. C.

Toxicity of solutions.—To determine if the fact discovered by NÄGELI, that insoluble solid substances placed in poisonous solutions in which algae are growing reduce the toxicity of the solutions, holds also for fungi, Miss FITCH[15] has investigated the action of insoluble substances upon media in which fungi were grown. Penicillium and Aspergillus were grown in pure cultures in beet decoction, in prune decoction, and in bouillon to which sulfuric acid had been added, making concentrations of $n/4$, $n/8$, $n/16$, $n/32$, $n/64$, and $n/128$. It was found that such substances as glass in different degrees of fineness, sand, and filter paper reduce the degree of toxicity of the poisonous solutions. For example, in cultures of Aspergillus in beet decoction, $n/64$ and $n/128$ H_2SO_4 showed stimulation, while $n/32$ was near the border line of beginning toxicity; but with the addition of glass $n/32$ showed the greatest stimulation of growth of the series, and a concentration as high as $n/16$ still showed marked stimulation. All other experiments showed results of the same nature, thus establishing the fact that the principle of NÄGELI holds in this case, as it has been shown to hold for flowering plants. Such results were to be expected, since the modifying action of the solid substances is exerted on the solution and not on the organisms growing therein.—H. HASSELBRING.

Glycogen and sporulation in yeast.—KOHL[16] finds that glycogen is more abundant in actively budding cells of *Saccharomyces cerevisiae* which he examined than it is in the resting cells. In view of this fact he believes that glycogen is not exclusively a reserve product, but that it represents an intermediate product in the formation of alcohol from sugar. He suggests that glycogen is broken down to glucose and isomaltose, which undergo splitting into alcohol and CO_2 by the action of zymase, and that the hexoses consequently first undergo transformation into glycogen in the process of alcoholic fermentation. In other fungi also KOHL finds that glycogen is not primarily a storage product; it does not appear in the spores of the Mucorales nor in sclerotia until germination or growth has begun. In the same paper KOHL gives some preliminary observations on the sporulation in yeast. The young spores are frequently surrounded by fatty substances in the early stages of formation. The nucleus divides amitotically both in budding and in spore formation, and one to four spores are formed. In the first case the cell nucleus becomes the spore nucleus directly. Often a nucleus which does not produce a spore remains in the cytoplasm of the mother cell after the spores are formed.—H. HASSELBRING.

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[15] FITCH, RUBY, The action of insoluble substances in modifying the effect of deleterious agents upon the fungi. Ann. Mycol. **4**:313–322. 1906.

[16] KOHL, F. G., Ueber das Glykogen und einige Erscheinungen bei der Sporulation der Hefe. Ber. Deutsch. Bot. Gesells. **25**:74–85. *pl. 1. figs. 2.* 1907.

Supernumerary pollen grains of Fuchsia.—BEER[17] has investigated Fuchsia, whose pollen mother cells are recorded as producing five to fourteen microspores. He found frequently six to ten microspores within a single cell, and a study of the nuclear divisions led to the conclusion that these high numbers are due to the occurrence of irregularities in the distribution of the chromosomes during anaphase, as described by JUEL for Hemerocallis. The chromosomes move very unevenly toward the poles, and some, either singly or in groups, lag behind and often become cut off entirely from the two main chromosome groups. Usually these separated chromosomes give rise to distinct nuclei, which vary in size according to the number of chromosomes they contain. During the second division the small as well as the large nuclei produce distinct spindles and divide. The second division is much more regular than the first, and no supernumerary nuclei were observed to originate at this stage. The small pollen grains are as definitely organized as the large ones, so far as the usual walls and their composition are concerned.—J. M. C.

Embryo sac of Peperomia.—JOHNSON[18] has discovered in a delicate, shade-loving, Jamaican species of Peperomia (*P. hispidula*) an interesting variation of the well-known situation in *P. pellucida*. There is a single hypodermal archesporial cell, which cuts off a tapetal cell. The mother cell develops the embryo sac directly, the first four free nuclei being "arranged in a perfect tetrad." At the next division a distinct polarity is developed, two nuclei passing to the micropylar end of the sac, and the other six grouping at the antipodal end. At the next division the Peperomia condition of sixteen free nuclei is reached, four being micropylar and twelve antipodal. A well-defined egg and one synergid are organized, the two remaining micropylar nuclei passing toward the center of the sac, where they encounter the twelve antipodal nuclei. The whole group of fourteen nuclei fuses into one great fusion nucleus. The division of this fusion nucleus is accompanied by wall-formation, and an endosperm tissue of about forty cells is developed.—J. M. C.

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[17] BEER, RUDOLF, The supernumerary pollen grains of Fuchsia. Annals of Botany **21**:305–307. 1907.

[18] JOHNSON, D. S., A new type of embryo sac in Peperomia. Johns Hopkins Univ. Circ. **1907**:no. 3. 19–21. *pls. 5–6.*

Influence of external conditions on geotropic response.—A timely paper by BACH[19] records some valuable conclusions, of which perhaps the most important is that the length of the reaction time cannot be used as a measure of the amount of stimulation. The minimum presentation time found in a variety of species was two minutes, as compared with fifteen minutes found by CZAPEK. CZAPEK'S figure has thus far been widely accepted, but the lower values of the author are apparently good. The length of the plant is a factor if the plant is less than medium, in which case the reaction-time is lengthened. Temperature is a potent factor, even variations of 14–35°. Such variations have been regarded by CZAPEK as impotent, but the opinion was based on the behavior of different material. Either regular or irregular shaking are indifferent factors. Other important conditions tried were duration of stimulation, centrifugal force, positional deviations. The paper shows the guiding hand of FITTING, whose service is acknowledged. —RAYMOND H. POND.

Young sporophytes of Lycopodium.—Miss WIGGLESWORTH[20] has investigated the structure of sporelings of *L. complanatum* and *L. clavatum*, the material being obtained from Dr. BRUCHMANN and consisting of two sporophytes of each species. The first root may show monarch, diarch, and triarch arrangement in the same plantlet, the phloem occupying the center of the stele and extending between the xylem groups to its periphery. The roots arise endogenously near the apex of the stem and either pass out directly or downward through the cortex. At the base of the stem the vascular strands are continuous with those of the first root, and a fusion of two or of all three of the xylem strands occurs. The xylem strands take a very irregular course, fusing with one another and subdividing in the lower part of the stem. The upper part of the stem shows a triarch or tetrarch arrangement of xylem with central metaxylem, generally connected with two or more groups of protoxylem.—J. M. C.

Embryology of Rhytidophyllum.—COOK[21] has investigated the embryology of Rhytidophyllum (*R. crenulatum* and *R. tomentosum*), a genus of Gesneriaceae, the material being Cuban. The ovulate archesporium is a single hypodermal cell, which usually functions directly as a megaspore. The embryogeny is of the well-known Capsella type, differing only in certain features of dermatogen-formation and in the contributions of the hypophysis. The embryo encroaches upon both endosperm and nucellus, and in the mature seed is invested only by the integuments.—J. M. C.

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[19] BACH, HEINRICH, Ueber die Abhängigkeit der geotropischen Präsentations- und Reaktionszeit von verschiedenen äusseren Faktoren. Jahrb. Wiss. Bot. **44**:57–123. 1907.

[20] WIGGLESWORTH, GRACE, The young sporophytes of *Lycopodium complanatum* and *Lycopodium clavatum*. Annals of Botany **21**:211–234. *pl. 22.* 1907.

[21] COOK, MELVILLE T., The embryology of Rhytidophyllum. Bull. Torr. Bot. Club **34**:179–184. *pl. 10.* 1907.

NEWS

Professor F. H. Billings of the Louisiana State University has been appointed assistant professor of Botany in the University of Kansas.

A short sketch of the late Maxwell T. Masters, with portrait, written by James Britten, is published in *Journal of Botany* **45**:257–258. 1907.

Dr. E. B. Copeland declined the announced appointment at the University of West Virginia and immediately returned to his post in the Philippines.

Professor Francis E. Lloyd has been appointed chief botanist to the Intercontinental Rubber Company. Professor Lloyd's address will for the present be Torreon, Mexico.

Dr. Hermann von Schrenk has resigned from the U. S. Department of Agriculture, and has opened an office as consulting timber engineer at St. Louis. He has been appointed also pathologist of the Missouri Botanical Garden.

It is proposed to erect a memorial to the late Professor Leo Errera of the University of Brussels. American botanists who wish to contribute are requested to send their subscriptions to M. J. Massart, 44 rue Albert de la Tour, Brussels.

Dr. Fritz Noll, professor of botany in the Agricultural College at Poppelsdorf and assistant professor of botany in the University of Bonn, has been appointed professor of botany and director of the botanic garden at the University of Halle.

A new quarterly journal has been announced by Williams and Norgate (14, Henrietta Street, Convent Garden, London W. C.), bearing the name *Rivista di Scienza*. It is to be "an international review of scientific synthesis," the desire being "to coordinate the work carried on in different fields of knowledge." It will be issued in two editions: an international edition, in which each article will appear in the language of the author; and an Italian edition, in which the German and English articles will be translated. In the list of writers for the first numbers the names of the following botanists appear: Darwin, Haberlandt, Pirotta, Solla, Wettstein, and Wiesner. The subscription price is 20 shillings.

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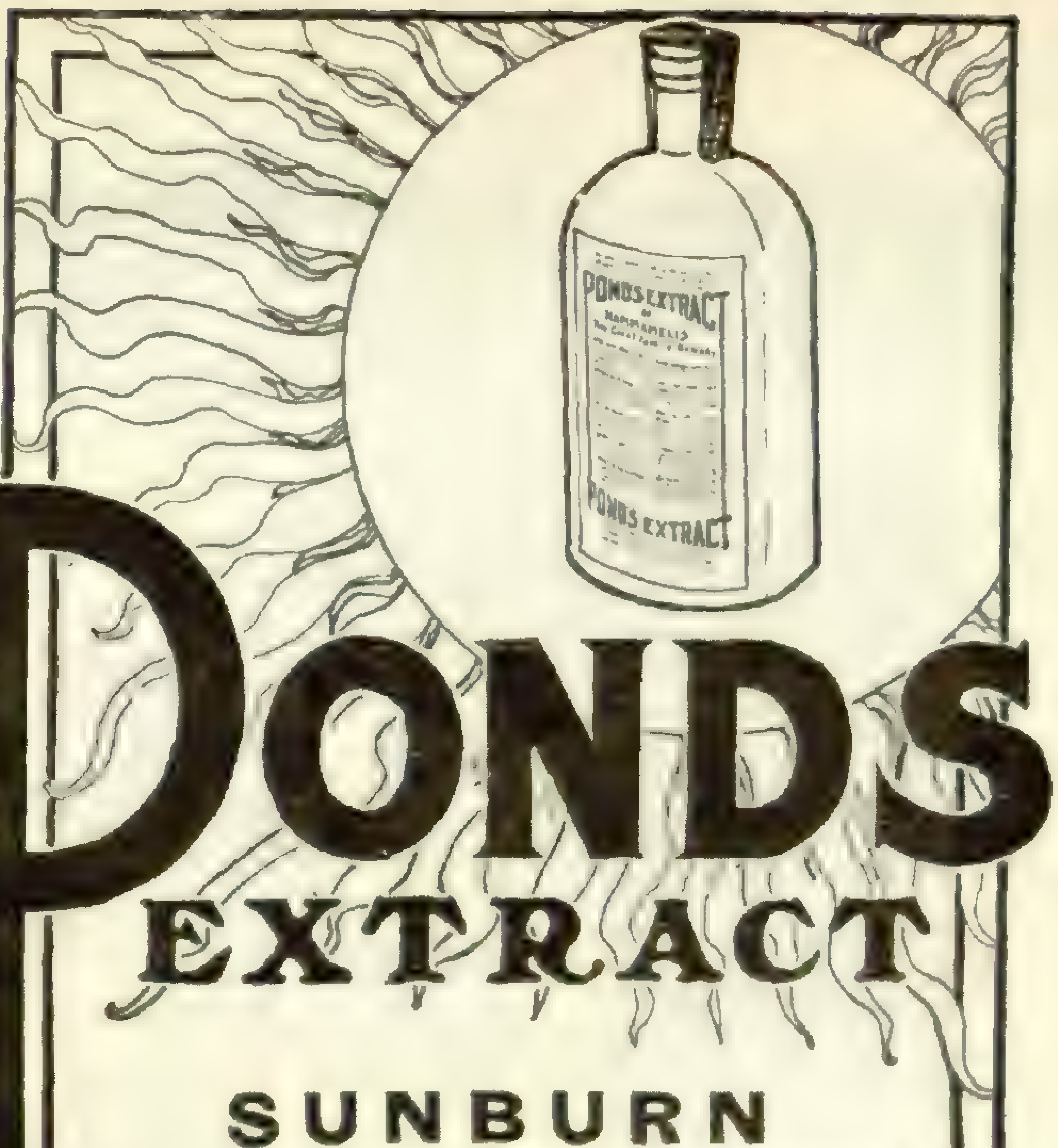

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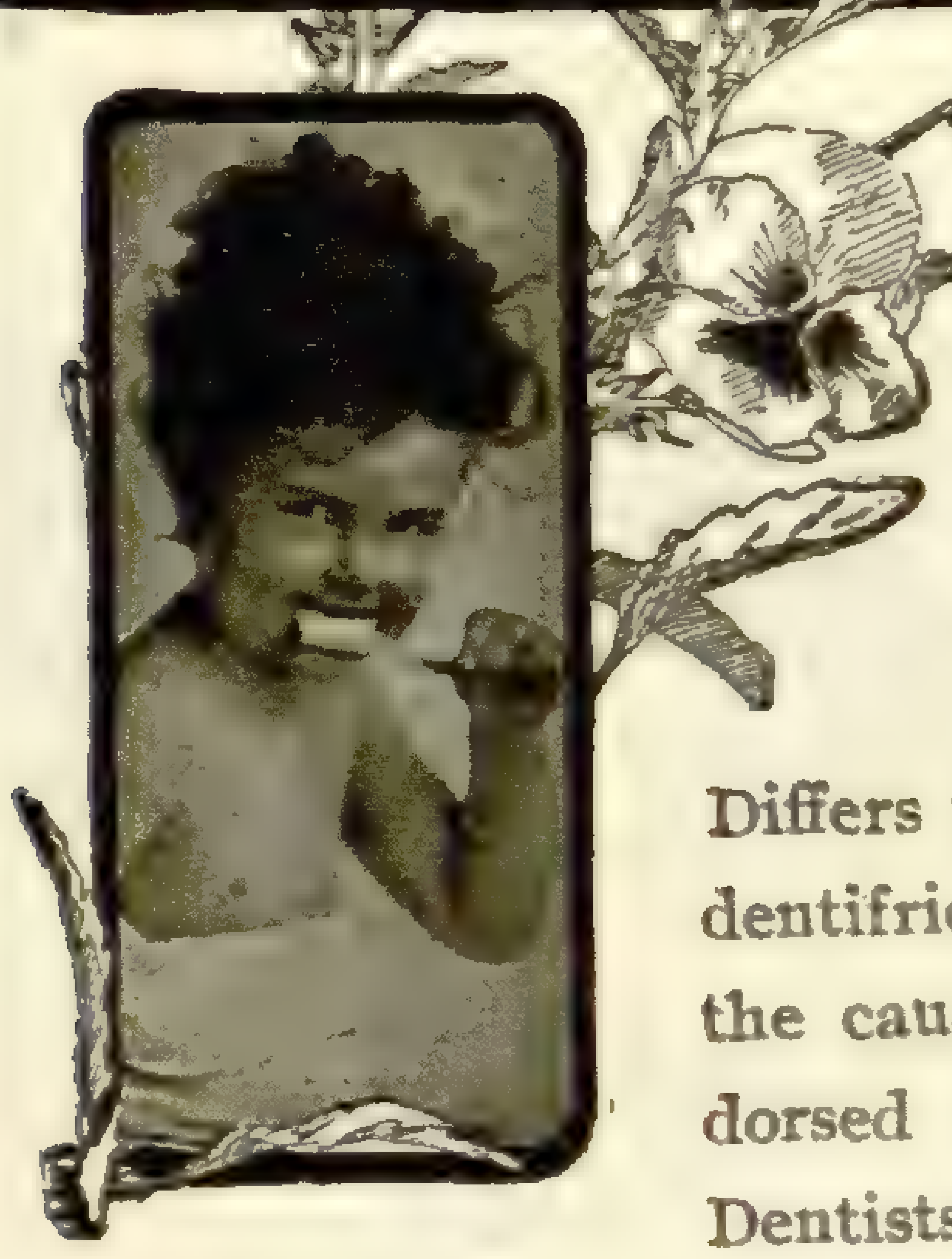

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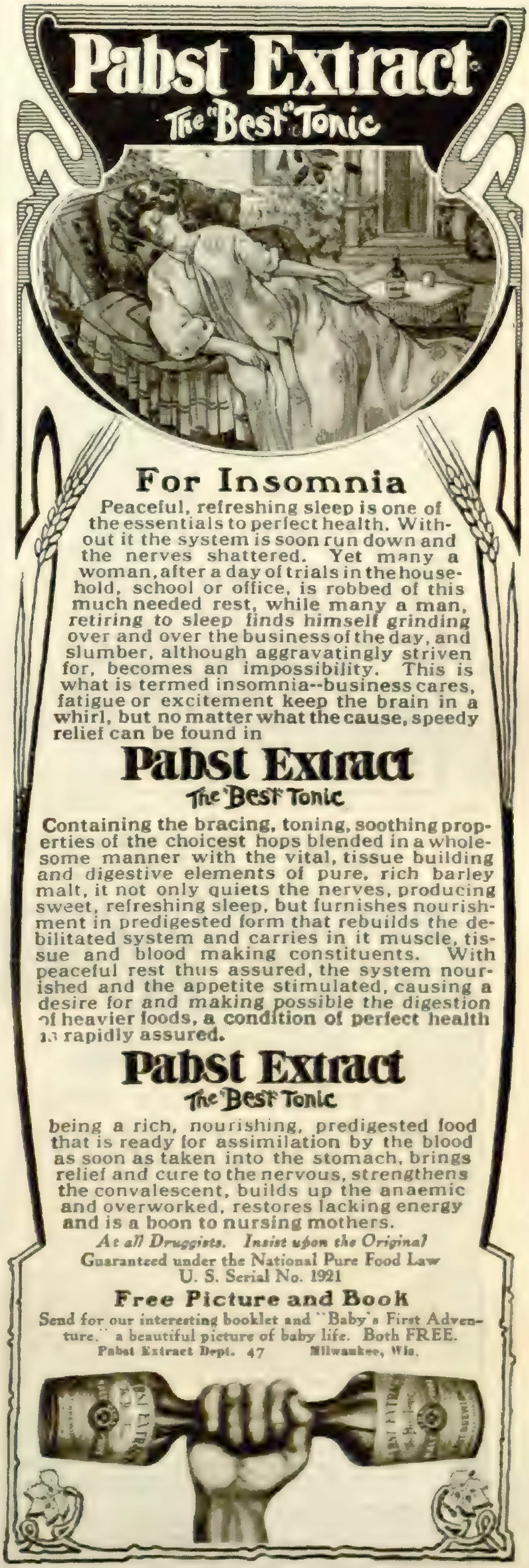

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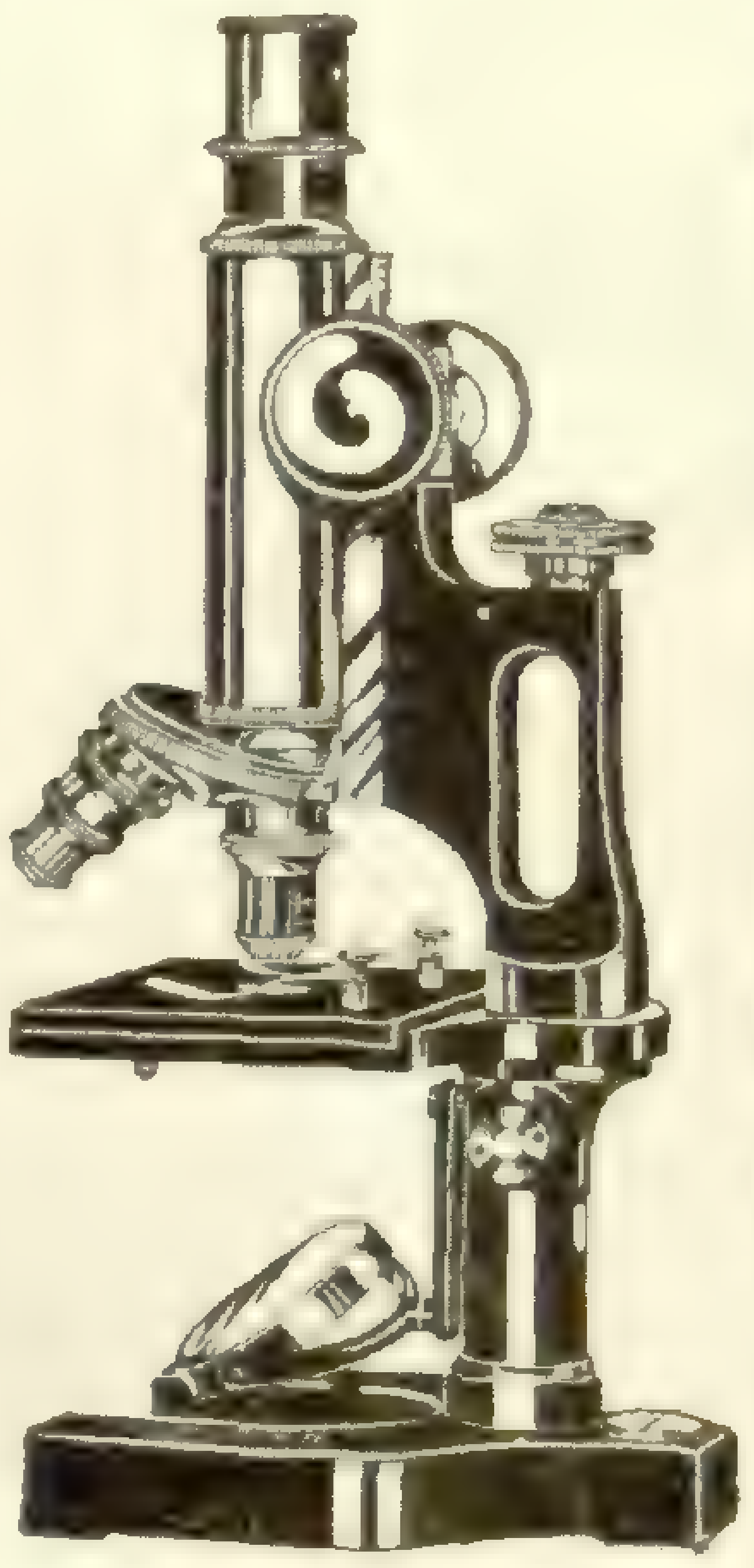

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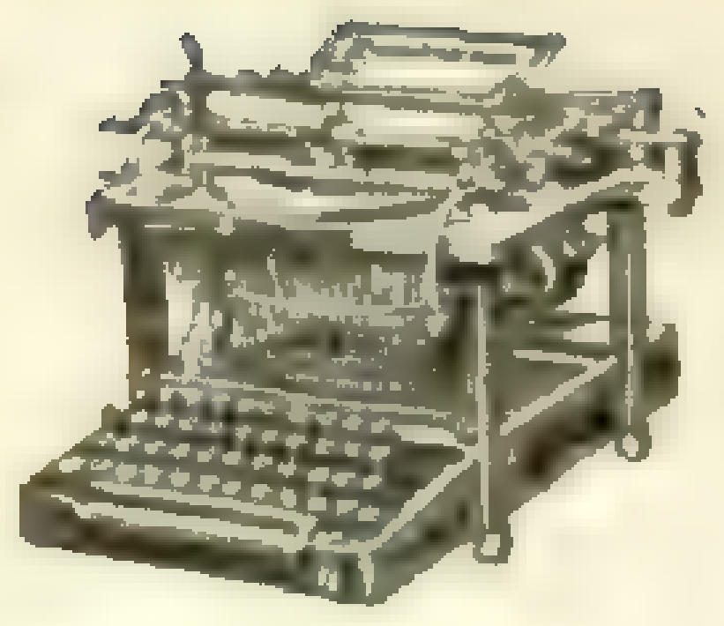

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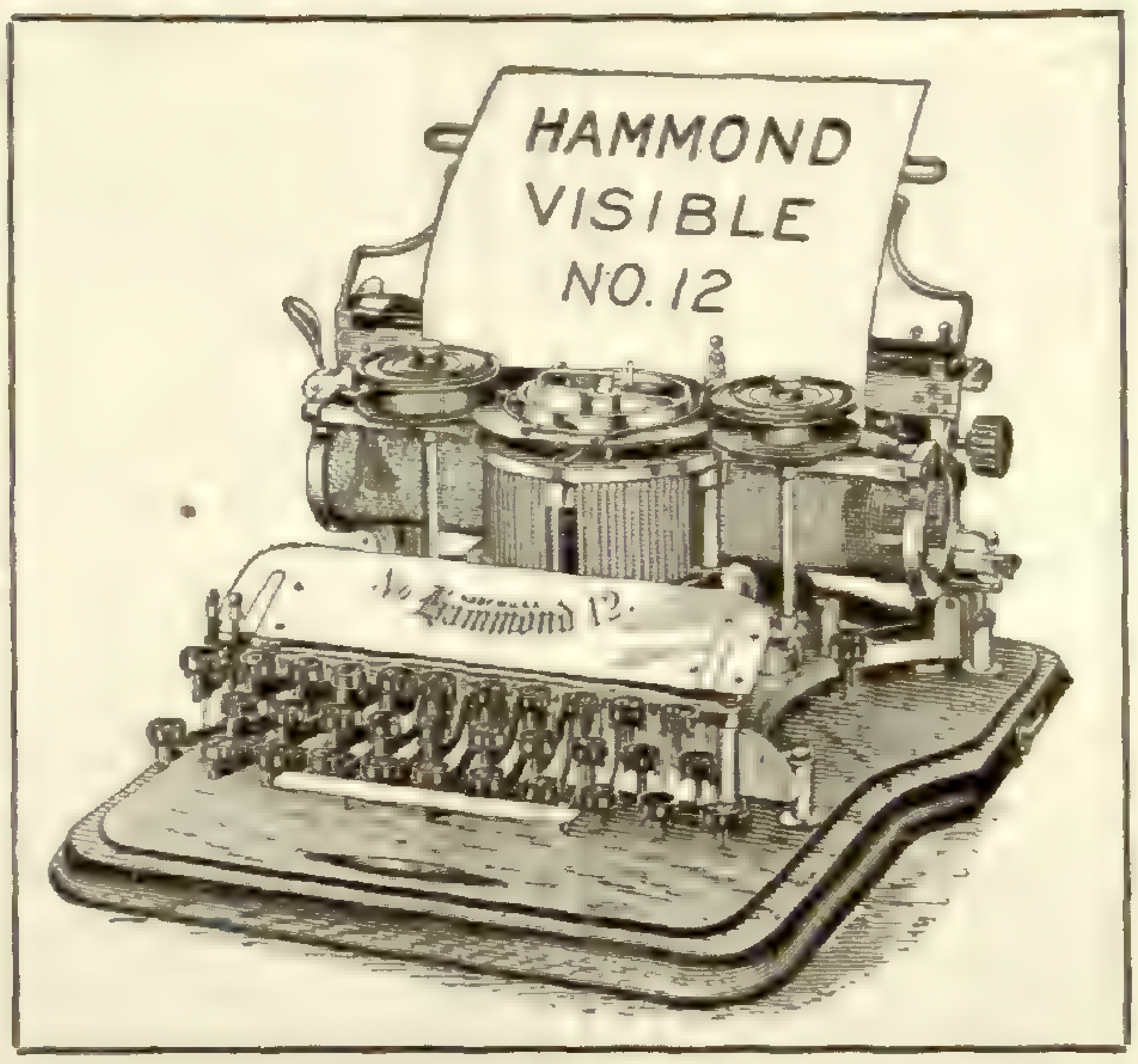
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September 1907

Editors: JOHN M. COULTER and CHARLES R. BARNES

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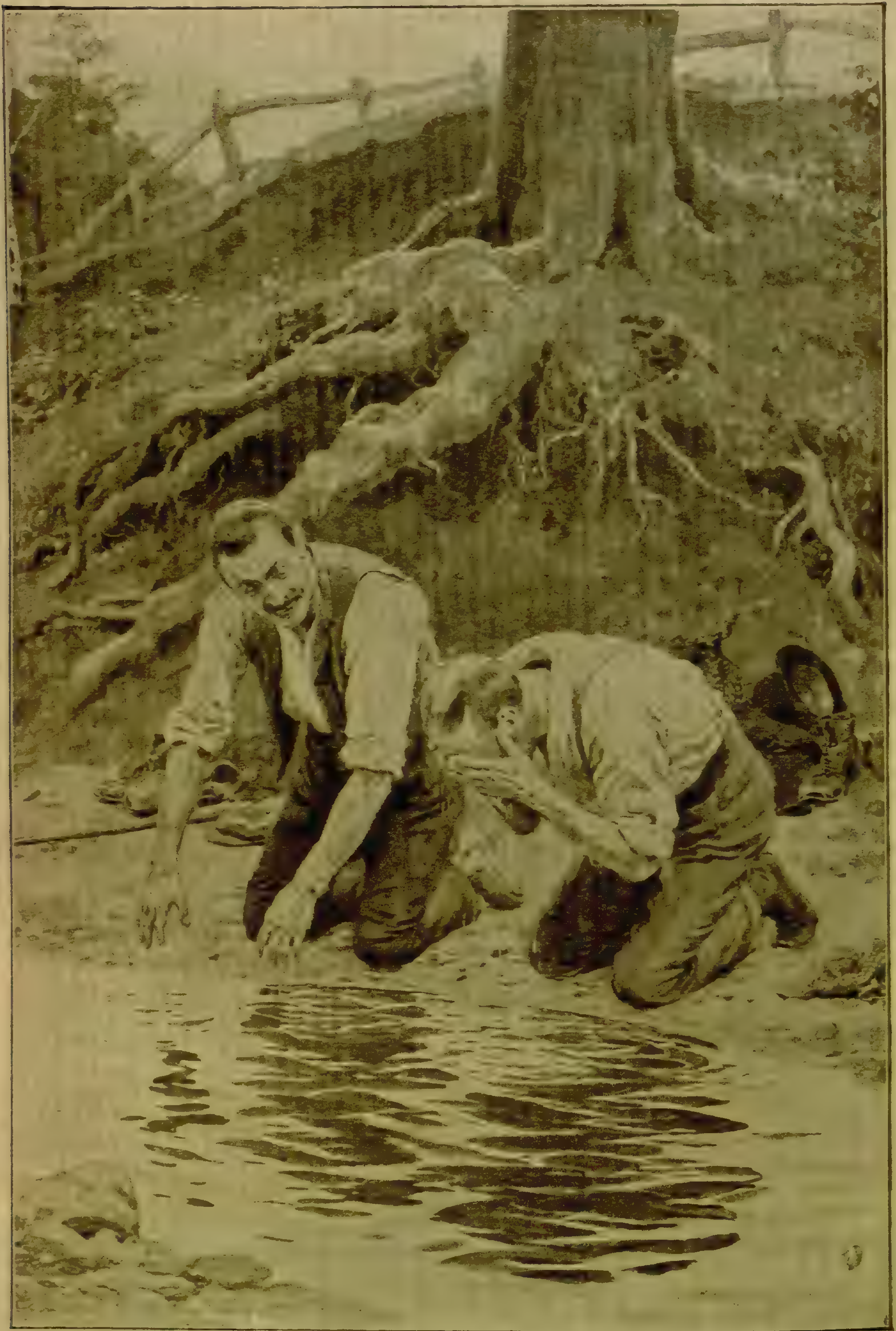
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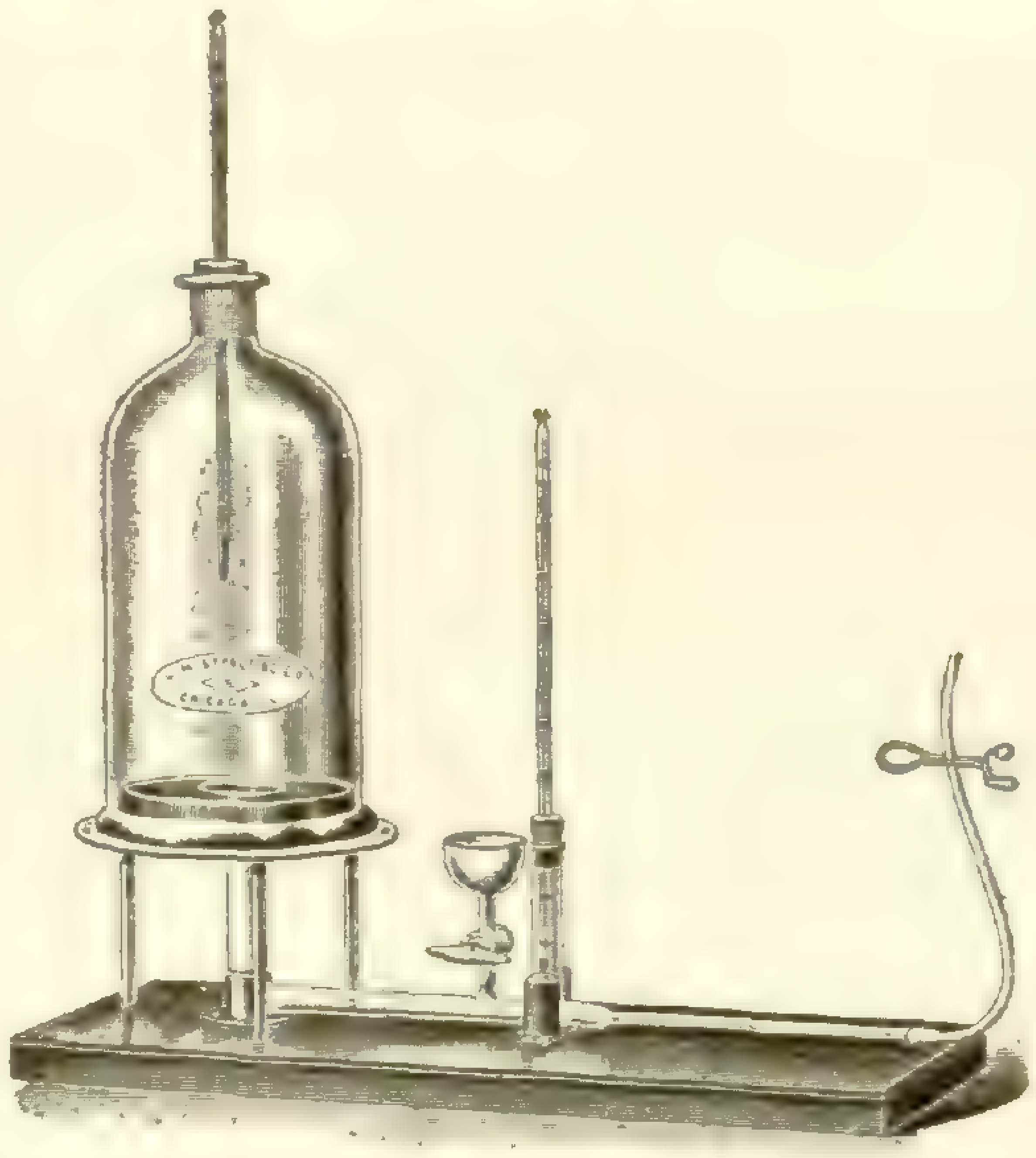

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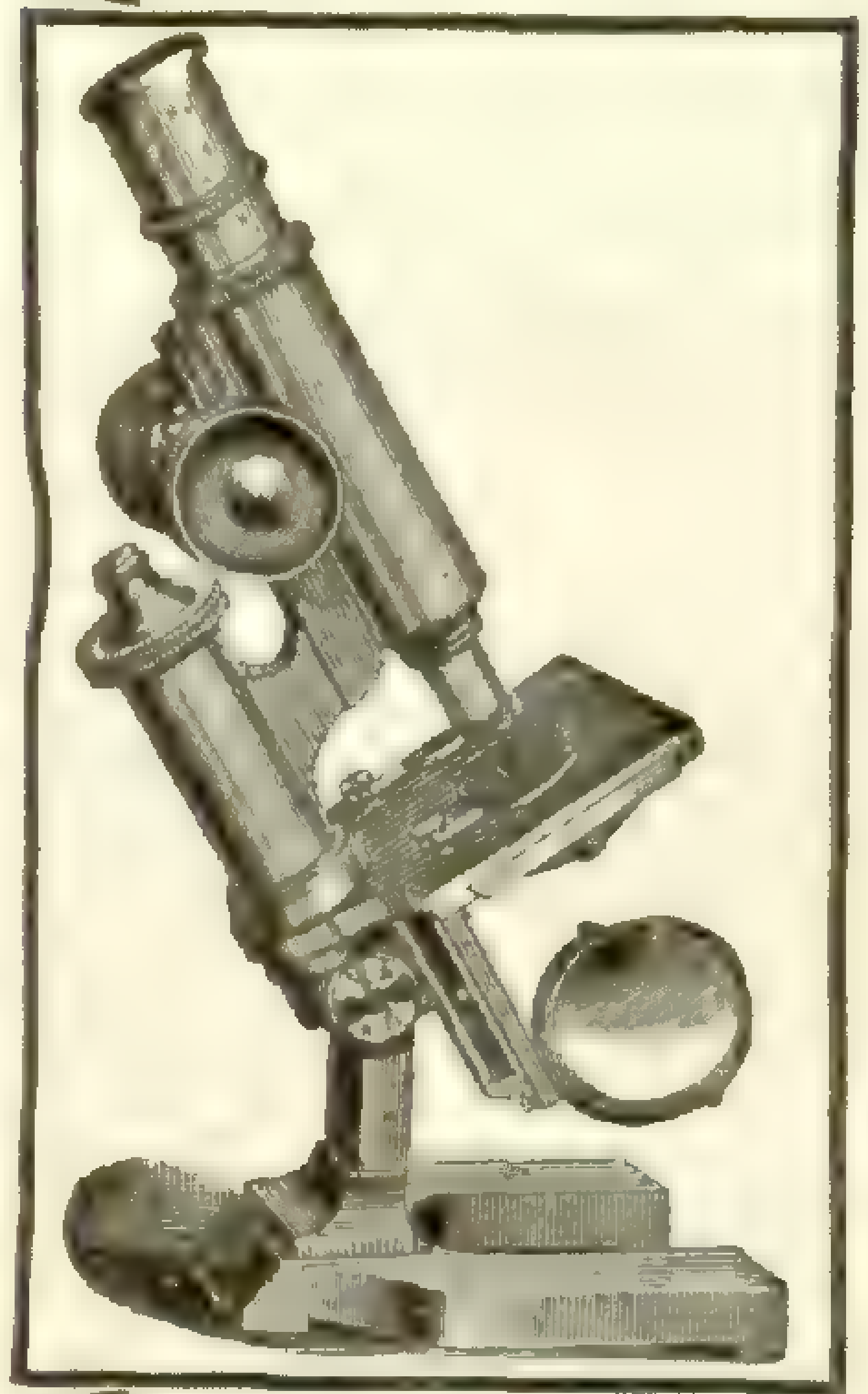

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VOLUME XLIV NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER 1907

THE STRUCTURE AND RELATIONSHIPS OF THE POTAMOGETONACEAE AND ALLIED FAMILIES[1]

MINTIN ASBURY CHRYSLER

(WITH PLATES XIV–XVIII)

In the alluring search for primitive monocotyledons which shall throw light on the vexed question of the origin of the group, the Helobiae have received much attention, including as they do such a wide range of forms, reaching from great simplicity to considerable complexity. It is generally agreed that those monocotyledons which possess a stocky rhizome or bulb have reached a degree of specialization which renders them less favorable for a study of primitive features than are the forms which have a more elongated axis showing distinct nodes and internodes. The Potamogetonaceae are prevailingly of the latter class, and the genus Potamogeton has been considered by SCHENCK (**27**) and others to represent a number of stages in the evolution of aquatic monocotyledons from ancestors which inhabited marshy ground. It has been more than once suggested that the monocotyledons have been derived from dicotyledonous ancestors through adaptation to an amphibious mode of life, so that the genus Potamogeton deserves study from all standpoints. A quite different view of the origin of monocotyledons has been proposed by CAMPBELL (**3**), who seeks to link the group with heterosporous Filicineae, especially Isoetaceae, through such forms as Naias.

It is proposed in the present paper to discuss certain features of the structure of Potamogeton which have apparently been overlooked, but which seem to be significant from the standpoint of phylogeny; also to bring together the salient points concerning the structure of the other genera of the family, so that if possible their relationships may be worked out. A few genera belonging to allied families have been included in the account.

---

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 9.

I wish here to record my obligations to the following, who have very kindly supplied me with material: Professors G. F. ATKINSON and W. W. ROWLEE and Mr. H. H. SMITH, of Cornell University, Mr. H. H. BARTLETT of the Gray Herbarium, Mr. J. G. HALL of the North Carolina Experiment Station, Mr. A. JEFFREY of Toronto, Dr. R. G. LEAVITT and Mr. A. A. EATON of the Ames Botanical Laboratory, Mr. C. P. SMITH of Carmel Bay, Cal., and especially to Professor M. L. FERNALD of the Gray Herbarium, who has been kind enough to determine most of the species employed in the research.

Potamogetonaceae

In this family the following genera have been accessible for study from preserved material: Potamogeton (thirteen species), Ruppia, Zostera, Phyllospadix, Cymodocea, Zannichellia. Celloidin was found to be the most favorable imbedding material for all except the smallest forms, for which paraffin was used. Serial sections through the nodes and other critical regions were in all cases studied.

POTAMOGETON

THE LEAFY SHOOT.—The mode of origin of this member has been carefully worked out by IRMISCH (**12**), who distinguishes between main shoots and reserve shoots. The internal structure of the upper internodes of such shoots varies somewhat widely in the different species, and upon the basis of the characteristics as revealed by a cross-section, together with the leaf structure, RAUNKIAER (**21**) has proposed a classification of the species and devised a convenient key. The differences between the species consist in the presence or absence of cortical bundles, and in the degree of union of the strands which compose the vascular part of the central cylinder. *Fig. 11* shows at low magnification the structures occurring slightly above one of the upper nodes of the leafy shoots. At the upper side of the figure is the section of the petiole with its median and lateral traces. Below this are the two fused stipules, sheathing the stem; their main bundles are barely visible at this magnification, but are situated at the angular swellings. Between the stipules and the stem is an axillary bud. The stem shows the lacunar cortex characteristic of aquatics, and a well-developed central cylinder. *Fig. 13* shows certain of these features more clearly, and also makes visible the numerous cortical strands which lie in the angles of the meshes.

Since the course of the leaf traces furnishes a key to the structure of the internodal stele, it is proposed to describe the course of the bundles in a well-developed species, *P. natans*. Stated briefly, the seven or more leaf traces shown in *fig. 11* fuse to form three, which enter the central cylinder, pass down through one internode separately at the periphery of the central cylinder (see DEBARY **7**, p. 270.), then approach one another, pass down through a second internode in the form of what may be styled a "trio" of bundles, and at the third node become indistinguishable on account of union with the bundles of the central cylinder. Since the leaves are arranged alternately in two vertical rows, there are two groups of leaf trace bundles in the cross-section of any internode. This is illustrated in *fig. 14*, which will be rendered clear by the following diagram (*fig. 1*), in which t_1, T_1, t_1 represent the traces of the next higher leaf, t_2, T_2, t_2 those of the second higher leaf, while the remaining bundles are those which are styled by DEBARY cauline, since they do not lead directly to any leaf. Although the petiole contains seven or more bundles, as shown in *fig. 11*, they enter the central cylinder as three, since the lateral bundles on each side fuse with one another. On each side this fusion bundle is joined also by the median bundle of the stipule of that side. An anastomosing branch may be sent to the median leaf trace. The bundles at the base of the petiole, like those of the internode, are devoid of xylem, but a lacuna represents the absent vessels, and shows that the bundle is collateral. As the bundle enters the cortex of the stem, ringed vessels or tracheids make their appearance, and the bundle becomes somewhat swollen and almost amphivasal, owing to increase in the number of tracheids which come more and more nearly

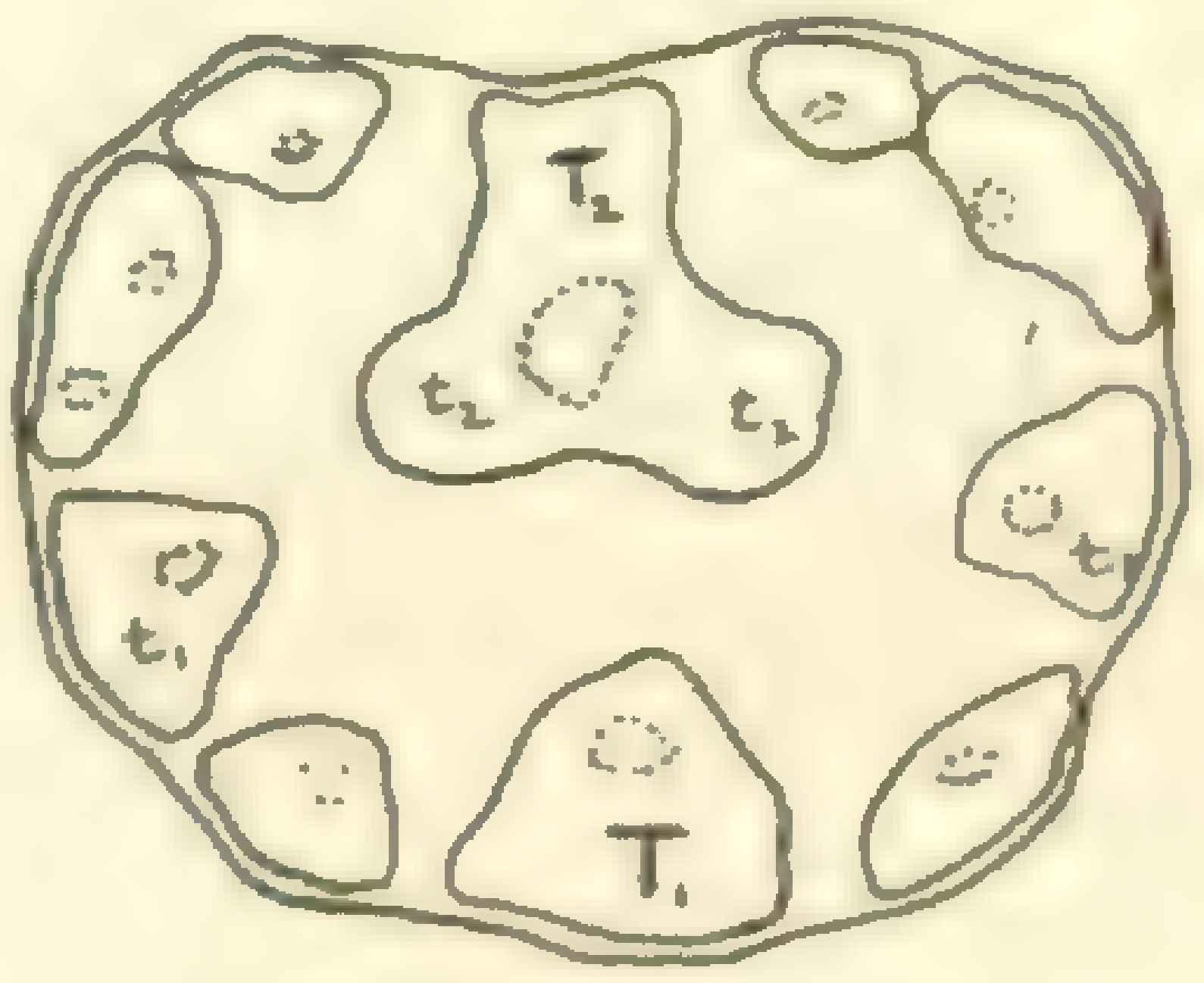


FIG. 1

to surround the phloem, thus recalling the condition found by the writer in grasses (**6**), where, however, the appearance is more pronounced. With the three foliar traces groups of mechanical fibers enter the central cylinder. After anastomosing with other bundles present at the node, the three lose their xylem and proceed downward at the periphery of the stele, occupying the middle region of three contiguous sides of the roughly oblong section of the stele (*fig. 14*). At the next node they enlarge, move toward the center of the stele, and the xylem again appears, first at the inner side of each bundle, filling the cavity, thence spreading around the phloem, so far as to render the bundle almost or quite amphivasal (*fig. 15*); the two lateral ones anastomose with other bundles, then the three approach, including between them an island of parenchyma which is surrounded by the xylem of the bundles. The xylem again disappears, as does also the island of parenchyma, which is replaced by a cavity which persists through the succeeding internode. Thus the "trio" is formed and descends to the next node, where tracheids appear once more, first around the cavity, and thence spreading around the bundles until the two lateral ones become amphivasal. At the same time the three bundles enlarge, the two lateral ones fuse, then separate, and all three join other bundles of the nodal complex, such as those of the axillary branch which enters at this level. Both the petiole and the fused stipules contain many small bundles consisting of fibers or of thin-walled cells or of both. These bundles descend into the cortex of the stem, some of them fusing with similar bundles of that region derived from petioles and stipules of higher leaves. In this way apparently arise the very numerous cortical strands characteristic of this species, and it may be stated in general that those species which possess a cortical system derive it from the petioles and stipules. Two points in the foregoing account seem worthy of emphasis, namely, the presence of amphivasal bundles wherever the leaf trace bundles are about to fuse with other bundles, and the very different course pursued by the leaf traces from that which is seen in most monocotyledons.

Concerning the insertion of branches it should be noted that the phloem of the bundles shows a remarkable enlargement just before joining the stele of the main stem, as is shown in *fig. 12*. The elements of the phloem at this point are narrow cells with very thin walls, quite unlike the well-marked sieve tubes which are seen in other parts of the stem. Such bundles are frequently seen to be amphivasal just before they are inserted on bundles of the main stele. Species with an axial cylinder like *P. natans* are: *P. perfoliatus*, *P. Nuttallii*, *P. praelongus*, etc.

P. natans has been chosen for the foregoing description, not because it presents the most primitive structure of any of the species, but because the vascular tissues are well developed, probably on account of the transpiration from the numerous and large floating leaves. What seems to be a more primitive disposition of the vascular bundles of the central cylinder is seen in *P. pulcher* (*fig. 19*), also a form with some floating leaves, but with broad submerged leaves instead of the phyllodes of *P. natans*. The course of the leaf trace bundles in *P. pulcher* resembles that already described, with the noticeable difference that the three bundles do not unite to form a "trio," but merely approach one another in the medulla of the second internode after the insertion of the leaf, giving the appearance shown in cross-section (*fig. 20*). A diagram (*fig. 2*) will make clear the topography of the central cylinder: as before, t_1, T_1, t_1 represent the traces of the next higher leaf; t_2, T_2, t_2 those of the second higher leaf; while the remaining bundles are cauline. As in the former species, amphivasal bundles occur at the nodes when two bundles are about to fuse. In spite of the liberal size of the leaves, and the fact that some of them float, no cortical bundles are present in the stem (*fig. 19*). Numerous small bundles are present in the stipules, but they turn abruptly inward and enter the central cylinder, while the median bundle of each stipule as usual joins the lateral leaf trace.

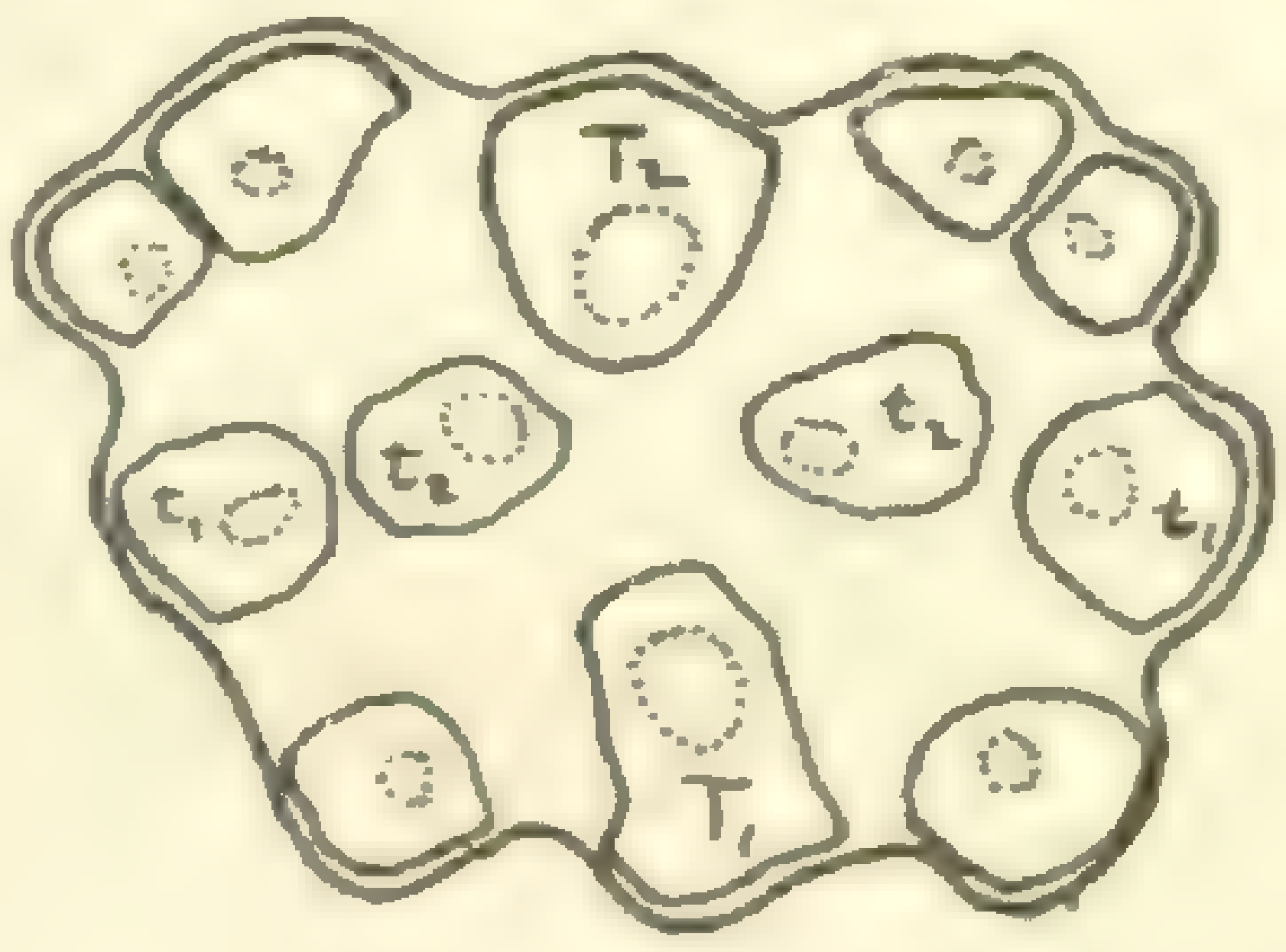


FIG 2

The two species already considered represent two types of central cylinder found in the genus. They are evidently closely related, and the *natans* type may evidently be regarded as derived from the *pulcher* type by the partial fusion of the three leaf traces during their descent through the central cylinder. At least two other types may be distinguished, in one of which the bundles of the central cylinder have further fused so as to form three more or less clearly separated areas, as is shown in the photograph of *P. crispus* (*fig. 28*) and in *fig. 3*. T_1, t_2, T_2, t_2 of the preceding diagrams have united to form the central area, while the remaining bundles form the lateral regions. T_1 may be distinguished from T_2 by the double lacuna of the central area. As usual, three (or sometimes five) leaf trace bundles enter the central cylinder, the large median one joining the central area, and the laterals, each composed as usual of bundles from the petiole and one from the stipule of that side, join the lateral areas of the central cylinder. DEBARY (**7**, p. 274) gives a singularly misleading description and inaccurate diagrams of this species, owing probably to the crudity of his methods of investigation. SCHENCK (**28**, p. 41) has given a correct interpretation of the appearances presented by a cross-section, and I have confirmed his statements by series of sections through the nodes. *P. crispus* is no more an "anomalous monocotyledon" (DEBARY) than are the other species of Potamogeton, since, as shown above, its vascular system can be easily derived from that of *P. pulcher*.

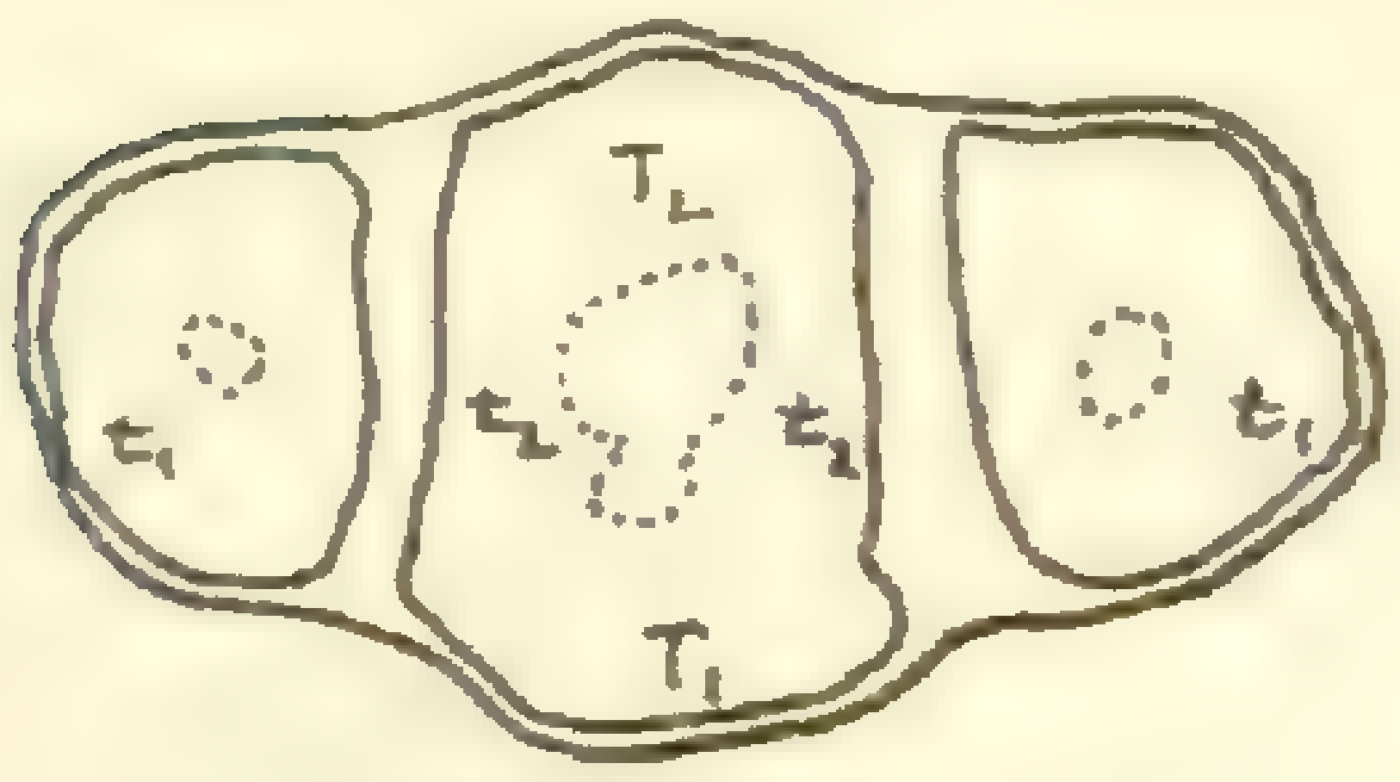


FIG. 3

A further reduction or fusion of the vascular elements is shown in the species of which *P. pectinatus* (*fig. 18*) may be taken as the type. In the internodes the xylem is represented only by a central cavity surrounded by parenchyma and phloem, but at the nodes a division of the stele into three areas is more or less plain. The last fact suggests that the condition found in this species has been derived from that seen in *P. crispus*, since ancestral characters are apt to persist at the nodes.

The behavior of the small bundles derived from the petiole and stipules shows great variation in the different species. (1) They may descend into the cortex of the succeeding internode, constituting the usually numerous cortical bundles of a number of species, e. g., *P. natans*, eventually joining others of the same kind, or finding their way into the central cylinder at a lower node. (2) They may descend a short distance into the cortex, then disappear, while a short distance below the node other strands make their appearance in the cortex, to disappear before the next node is reached, e. g., *P. Robbinsii*.

(3) They may (with the exception of the central bundle of each stipule, which joins a lateral leaf trace) disappear soon after entering the cortex, leaving the stem without cortical bundles, e. g., *P. crispus*. (4) They may enter the central cylinder immediately, like the leaf traces, leaving the stem devoid of cortical bundles, e. g., *P. pulcher*. To this should be added the peculiar case of *P. Nuttallii* (*fig. 5*), in the upper leaves of which the median bundle of each stipule fuses with the neighboring lateral leaf trace bundle, and from the fusion is given off a strand which descends into the cortex. The cortical bundles of this species are not numerous (six to eight), and form a complex anastomosis with the central cylinder at the level of the lower part of the node. In general it may be stated that when a species possesses cortical bundles they are derived from the small bundles of the petiole and stipules. This view is confirmed by the fact that such bundles are universally present in the petioles and stipules, even when they are absent from the stem. As to composition, the cortical bundles range from complete collateral bundles to mere groups of a few fibers, and moreover the character of a bundle may change greatly in its course, being composed mostly or altogether of phloem at one level and only of fibers at a slightly different level. SCHENCK (**28**, pp. 48, 54) is of the opinion, and my observations confirm his view, that all these strands represent real fibrovascular bundles, which share in the reduction shown by the vascular tissues of the central cylinder.

The extent to which mechanical tissue is present is, according to SCHWENDENER (**30**), dependent on whether the plant grows in still or in running water. But different species occupying a similar habitat may differ widely in respect to the presence of mechanical tissues; for example, *P. natans* is abundantly provided with cortical strands, while *P. pulcher* entirely lacks them, yet both are inhabitants of ponds, and both possess floating leaves. Judging from over forty species for which data are available, there is no relation between the presence of cortical bundles and a totally submersed or a partly floating habit. Neither can a relation be established between size of leaf or stem and presence or absence of cortical bundles. That these strands are not primitive structures, but have arisen in connection with the mechanical necessities of the leaves and stipules is indicated by three facts. (1) In the creeping stem, which has rudimentary sheathing leaves devoid of stipules, the small cortical strands are few and wanting, even in species which possess them abundantly in the leafy shoot. (2) As will be pointed out later, in *P. natans*, *P. Nuttallii*, etc., the cortical strands spread upward into the peduncle, but fuse with the strands of the vascular ring (see below) or fade away soon after reaching the fertile part of the axis. (3) As stated above, small bundles are of constant occurrence in the petioles and stipules, even if the stem is free from them.

THE CREEPING STEM.—According to IRMISCH (**12**), this does not represent the main stem, but certain lateral members of the extensively branched system. The structure differs in several noteworthy respects from that of the leafy stem. The central cylinder is flattened in accordance with the dorsiventral nature of the stem, as is seen in the photograph of *P. pulcher* (*fig. 21*), and presents a truly dicotyledonous looking ring of collateral bundles (*fig. 22*), though the appearance is somewhat masked by the large size of a dorsal and a ventral bundle. These two bundles may meet in the center of the stele in case the stem is much flattened. All of these are cauline strands, whose disposition is practically unaffected by the entrance of the insignificant leaf traces from the thin deciduous scale leaves. Hence there is no "trio" of bundles, and the disturbing elements are branches, not leaves. Considering a node lacking a branch, the large dorsal and ventral bundles are seen in a series of sections to pass through the node sometimes without anastomosis with other bundles; they swerve slightly toward the middle of the stele, while the lateral bundles partly close the gaps thus left in the vascular ring, and give off roots on all sides of the stele. In case a branch is present at a node, the dorsal and ventral bundles not merely approach the center of the stele but become much enlarged owing to excessive development of phloem (*fig. 17*), and fuse to form a large amphivasal strand which then breaks up into several amphivasal bundles. These anastomose with peripheral bundles of the stele and with the bundles of the branch which enter at this point. The bundles at the base of the branch likewise show a greatly swollen phloem, which is a conspicuous feature in the figure. It will be recalled that owing to the distichous arrangement of the leaves, the ascending stem shows two bundles on opposite sides of the central cylinder, which bundles are the median traces of the two next higher leaves. In the creeping stem, however, the two opposite bundles are seen from the foregoing to be connected with the origin of branches. As in the leafy shoot, vessels are present only at the nodes, and are represented by a cavity elsewhere. The endodermis is plain, of U-form, and suberised. *Fig. 16*, representing the creeping stem of *P. natans*, which should be compared with *fig. 13*, shows another point of difference between the creeping and the leafy stem. While cortical bundles are abundant in the latter, they are much scarcer or absent in the former, owing apparently to poor development of leaves and the absence of stipules. In case cortical bundles are absent in the leafy shoot, they are lacking also in the creeping stem, as may be seen from the figures of *P. pulcher*. In accordance with the sheathing character of the reduced leaves, the leaf traces enter the central cylinder separately, as may be well seen in *P. perfoliatus* or *P. heterophyllus*, which have better developed basal leaves than has *P. pulcher*.

THE FLORAL AXIS.—SCHENCK (28) and others have not failed to notice that the peduncle has a different disposition of bundles from that in the leafy shoot, but the earlier observers have apparently overlooked the regularity in the arrangement of the bundles. *Fig. 23* shows the appearance of a section through the fertile part of the floral axis of *P. natans*. The arrangement is evidently circular, and the bundles are collateral. Branches leading to the flowers do not have a gap above their point of exit, but spring from one bundle or from two adjoining bundles. Well-developed tracheary tissue is present in all of the bundles, in marked contrast to the condition seen in an internode of the vegetative axis. *Fig. 24* represents an appearance which occasionally occurs; here the bundles constitute a nearly closed vascular tube. The circular arrangement of bundles occurs in every species which I have examined, even in such slender forms as *P. hybridus*, the peduncle of which shows four separate strands, each surrounded by an endodermis (*fig. 26*). The basal part of the axis shows the same arrangement as that represented in the figures, but the strands are apt to be more widely separated. Cortical strands are also present in the peduncle of species such as *natans*, which show many such strands in the leafy stem (*fig. 25*); they either join bundles of the circle or dwindle away shortly after reaching the fertile part of the axis. A ring of collateral bundles in the floral axis of Eleocharis is figured by PLOWMAN (**19**), and is stated by him to be characteristic of the Cyperaceae. A similar condition is found in Triglochin (see below). The resemblance of these axes to the stems of dicotyledons can hardly fail to be noticed, and I am inclined to attach phylogenetic importance to the feature, rather than explain it on physiological grounds, as is suggested by SCHENCK (**28**). The persistence of ancestral features in the reproductive axis has been pointed out by SOLMS-LAUBACH (**31**) and by SCOTT (**29**), and the status of this as a general principle has of late received strong confirmation, especially from the work of JEFFREY, who in his memoir on the Abietineae (**14**) sums up the evidence in favor of the principle. In Potamogeton we seem to have another case in point, for the peduncle shows the primitive dicotyledonous arrangement of bundles, which moreover are collateral throughout their course.

GENERAL.—The affinities of the genus Potamogeton may best be discussed later, but we may here consider the relations of the species. The main question at issue is as to whether the species with large floating leaves or those with small submersed leaves are primitive, or whether, as RAUNKIAER (**21**) believes, the species with large submersed leaves are to be so regarded. One criterion for the decision of the question is the structure of the central cylinder in the various species. In his admirable memoir on submersed plants SCHENCK (**28**) has described and figured the central cylinder of a series of species, starting with *P. perfoliatus*, in which the bundles of the internodal stele are separate, and ending with *P. pectinatus*, in which the stele consists of thin-walled cells surrounding a central cavity, and he concludes that the series represents a process of fusion and reduction of the vascular tissues. In another work (**27**) the same author expresses the view that the pondweeds have sprung from terrestrial plants which passed through the amphibious, then the swimming, and finally the submersed stage: "*P. natans* würde nach dieser Ansicht die ursprunglichste Form unter den heutigen Arten noch vorstellen." With the general principle of reduction here stated the present writer is in accord, but it seems to him that the place of honor should be awarded to some such species as *P. pulcher* for the following reasons: (1) *P. natans* has some of its submersed leaves specialized as phyllodes, while in *P. pulcher* the submersed leaves are broad and differ from the floating ones mainly in their thinness; (2) It is probable that the separate bundles in the central cylinder of *P. pulcher* represent a more primitive condition than the "trio" of *P. natans*. There seems to be every reason to believe that the small-leaved submersed forms with a stem showing a concentric stele are to be regarded as simplified by reduction. Further, the group of species with stipules adnate to the petiole represented by *P. filiformis*, *P. pectinatus*, and *P. Robbinsii* are probably quite specialized forms, since they are connected with such forms as *P. natans* by a small group including *P. spirillus* and *P. hybridus*, in which the stipules are slightly adnate and the spikes are of two kinds, the emersed ones cylindrical, and the submersed ones capitate, consisting of four to six flowers. It should also be noted that *P. Robbinsii*, etc., have their flowers in an interrupted spike.

RUPPIA MARITIMA

This monotypic form has been uniformly placed in the same family as Potamogeton on account of its emersed inflorescence, perfect flowers, and alternate leaves. The complex arrangement of branches characteristic of Potamogeton is here represented by a creeping axis giving off roots and leafy shoots, as described by IRMISCH (**12**). The structure of the stem is comparatively simple: inside a lacunar cortex is a central cylinder of the type of *P. pectinatus*, viz., with a central cavity surrounded by small thin-walled cells. Tracheids are present at the nodes. Each leaf possesses a central bundle and two very slender lateral ones. The central bundle enters the central cylinder directly, as in Potamogeton; while the lateral bundles descend into the cortex of the stem for a greater or less distance, though they do not reach the next lower node, but dwindle away and disappear, as is illustrated in the diagram, *fig. 9*. This condition has in all probability been derived by reduction from that in which the cortical bundles joined the central cylinder at the next node below the insertion of the leaf to which they belong, for it is unreasonable to suppose that the leaf traces should originally have had no connection with the main conducting channels of the stem. Thus the cortical bundles of Ruppia belong to VAN TIEGHEM's second group (**32**, p. 751). The course of these bundles, and the occurrence of xylem at the nodes, as well as the filiform leaves and submergence of all parts of the plants except the flowers, leads to the view that Ruppia is an example of simplicity by reduction.

POSIDONIA

Magnus has given a short account of the stem structure of *P. oceanica* (**17**). According to his description, the conducting tissue of the central cylinder is flanked by a mass of mechanical fibers, and the cortex contains numerous small bundles of fibers and also a few conducting bundles. No account is given of the course of the leaf traces, and material has not been obtainable so far for the present research.

ZOSTERA

The widely distributed species *Z. marina* has been the subject of frequent study. Eichler (**10**) described the sympodium of floral axes, and Sauvageau (**23**) has given the best account of the vegetative structures of the five species, referring to the older literature on the subject. The creeping stem is monopodial, and bears the long ribbon-shaped alternate leaves, while the ascending branches are sympodes bearing the flattened spadices. In all these regions the main structural features are the same, namely, a wide, somewhat lacunar cortex containing two vascular strands and inclosing a narrow central cylinder. The structure of the last, however, differs considerably in the various regions of the plant. *Fig. 29*, from the lower part of the ascending shoot, shows the simplest condition, with a central lacuna and four masses of phloem, therefore representing four fused bundles. This condition is present also in the apical parts of the creeping stem, and arises from the distichous arrangement of the leaves. The older parts of the creeping stem show four additional bundles in the stele, alternating with the first-formed bundles. Xylem fills the lacuna at the nodal regions, but is nowhere well developed. From the sheathing base of a leaf a median bundle enters the central cylinder directly; while on each side two or more lateral traces fuse and join the cortical bundle on its side, which at the same level sends a branch to the central cylinder, as shown in the diagram, *fig. 6*. From the leaf also enter a large number of small bundles of fibers which run down in the outer region of the cortex; in the creeping stem these may be thin walled or even absent. The peduncle shows a structure similar to that of the stem figured; no circle of separate bundles such as in Potamogeton is found, but the central cylinder consists of two united bundles.

The well-defined cortical system of this plant is a characteristic feature which at once separates the genus from Potamogeton. In *P. Nuttallii*, however, we have a suggestion as to how the condition in Zostera may have arisen, as described above (p. 167); the lateral bundle entering the stem from the petiole and stipule may give off a branch which descends through the cortex. The chief difference between this condition and that in Zostera is that in the latter genus the cortical strand is continuous up and down through a number of internodes. Whether a leaf trace at once penetrates into the central cylinder, or descends at the periphery of the cylinder, or descends altogether outside the cylinder, appears to be a feature readily modifiable in the monocotyledons, as has been pointed out by the writer (**6**), and in almost every family of monocotyledons there are members in which at least some of the leaf traces pursue a cortical course for the length of an internode before joining the central cylinder. Apparently this condition is derived from that in which all bundles of the leaf trace join the stele directly.

According to SAUVAGEAU (**23**), *Z. Muelleri* and *Z. tasmanica* show two to five cortical bundles on each side in place of the single one of *Z. marina*. These bundles anastomose with one another at the node, and send a branch to the central cylinder, while receiving a single bundle from the leaf, i. e., the leaf has a median and only two lateral traces.

The affinities of this genus are by no means clear. Like Potamogeton it has an elongated inflorescence which here reaches a high degree of specialization. The totally immersed habit of the plant, together with the hydrophilous mode of pollination by means of filamentous pollen also indicate specialization. The vascular structures may have been derived from the condition found in Potamogeton, as is suggested above, but the resemblance is not striking, especially when we consider the eight radially arranged bundles of the central cylinder. The process of evolution has apparently separated Zostera far from its relatives.

PHYLLOSPADIX

This Pacific coast genus, nearly related to Zostera, has been inadequately studied, though DUDLEY (8, 9) gives a good general account, and corrects several mistakes of earlier writers, e. g., the supposedly tuberous habit of the base of the stem as erroneously figured in ENGLER and PRANTL (11). Through the kindness of Mr. C. P. SMITH, I have been able to study alcoholic material of *P. Scouleri* from Carmel Bay, California. As DUDLEY points out, the basal part of the stem, far from being tuberous, is an elongated rhizome, along which the leaves are arranged alternately right and left. In general plan, the structure of the stem resembles that of *Zostera marina*, showing a comparatively small central cylinder and two slender cortical bundles. To the latter the lateral leaf trace bundles are attached, while the median trace joins the central cylinder directly. These statements apply equally to the ascending stem, represented in *fig. 30*, which shows certain features more clearly on account of the absence of roots. As may be seen in the figure, two lateral traces enter the stem on each side of the median trace, and attach themselves to one of the cortical strands which then sends in a branch to the central cylinder. Thus the disposal of the leaf traces differs no more from that in *Zostera marina* than does this from other species of Zostera. The central cylinder is in most respects similar to that of Zostera, showing four bundles in a section through an internode of the ascending stem. In the upper part of such a stem the bundle derived from the median trace of a leaf runs somewhat apart from the other bundles of the central cylinder, and in general the vascular strands of this genus show a tendency to be more widely separated than in Zostera. The floral axis does not show the ring of bundles seen in Potamogeton, but these are arranged in a tubular stele, and there are two cortical strands as in the lower part of the stem. These features of the floral axis are in accord with its specialized character in this species. Numerous mechanical strands enter the stem from the leaves, especially in the ascending part of the stem, but they are not numerous nor thick walled in the creeping stem. As in Zostera the pollen is filamentous. The anatomical characters afford no reason for questioning the conclusion of DUDLEY, that the genus is derived from Zostera.

CYMODOCEA

This genus shows several points of resemblance to Zostereae, e. g., the filamentous pollen, elongated creeping stem, frequently ribbon-shaped leaves, and, as will be seen, its vascular structure is closely related. The best general account is that by BORNET (**2**) of the species *C. nodosa*, though the account of the vascular anatomy is meager. SAUVAGEAU has described certain features of the stem and leaf structure of a number of species (**24**). The only species accessible to me has been *C. manatorum*, and to it the following account applies. The internodal stem (*fig. 31*) shows a differentiation in its cortex which is characteristic of the genus. An outer zone free from lacunae contains near its inner limit a broken circle of cortical bundles, and surrounds an inner zone which is lacunar. The circle of bundles really consists of two sets, an arc-shaped group of four or five on each side of the central cylinder, which is somewhat flattened. Each of these groups corresponds to one of the two cortical strands of *Zostera marina*, and to the two to four strands of *Z. Muelleri* and *Z. tasmanica*. They are, as would be expected from analogy, connected with the lateral traces of the leaf, while the median leaf trace enters the central cylinder directly. At the node the cortical bundles of each side anastomose and send a branch which joins the central cylinder at the point of entrance of the median trace. Certain of these features are shown in *fig. 32*. As SAUVAGEAU figures for *C. serrulata*, the central cylinder consists of two bundles lying in the line which passes through the base of the leaf (*fig. 31*); the phloem contains several large sieve tubes, and the xylem of the two bundles is fused and is represented by a central lacuna. As the node is approached, tracheary tissue fills the lacuna, and at the point of entrance of the leaf trace that bundle of the stele lying toward the trace becomes amphivasal, quickly followed by the other bundle. After the entrance of the two bundles from the cortical system three amphivasal bundles are present in the stele, soon becoming two and changing to the collateral form as their xylem disappears and is replaced by the central lacuna. The cortical system of Cymodocea seems to be an extension of the plan seen in *Zostera marina*, *Z. Muelleri* forming an easy transition. The genus is to be regarded as a specialized one, judging from the anatomy and the filamentous pollen.

HALODULE

I have not examined material of this genus, but SAUVAGEAU'S account of the stem structure (**24**) leaves little doubt that it is derived from Cymodocea or one of its near ancestors. Instead of the arc of similar cortical bundles on each side of the central cylinder, Halodule shows one larger strand and a variable number of rudimentary strands forming an arc—apparently a more differentiated condition than that found in Cymodocea.

ZANNICHELLIA PALUSTRIS

The external morphology bears a general resemblance to that of Potamogeton, and the minor differences are stated in detail in IRMISCH'S classic work already referred to (**12**). The structure of the creeping and ascending stems is very similar, and carries the reduction observed in Ruppia a step farther. As stated by CAMPBELL (**3**) and confirmed by my observations, the central cylinder of the stem consists of thin-walled tissue inclosed in a distinct endodermis and surrounding a central cavity. The lacunar cortex lacks the two strands seen in Ruppia, for in Zannichellia the leaf contains a single trace which enters the central cylinder directly. Spiral tracheids are present at the nodes to nearly the same extent as in Ruppia, and are much more abundant than in *Naias flexilis* or *N. marina*. CAMPBELL makes the interesting observation that the filament of the stamen is traversed by tracheary tissue, showing in section usually two tracheids. The plant is totally submersed, and pollination is effected under water, a fact which points to a high degree of specialization. The single stamen and monoecious habit point in the same direction; in fact specialization and reduction are so great that the affinities of this monotypic genus are very uncertain.

Naiadaceae

NAIAS

On account of the simplicity and the exceptional development of its floral parts this genus has attracted much attention. Originally counted as belonging to Potamogeton, the tendency now is to put the genus in a family by itself. MAGNUS (**15**, **16**, **18**) has thrown much light on the morphology, and in his paper of 1870 gives an excellent account of the earlier work. CAMPBELL (**3**) has studied *N. flexilis* by the aid of modern technique, and RENDLE (**22**) has recently revised the genus from the systematic standpoint. The last two mentioned authors summarize our knowledge of the morphology, so we may at once proceed to a discussion of the features which throw light on the affinities of the genus. My own observations have been confined to two species, *N. flexilis* and *N. marina*, obtained from several different localities with a view to confirming earlier accounts. The structure of the stem resembles that found in Zannichellia, and is figured for typical species by RENDLE; a cortex containing a circular row of lacunae incloses a slender stele which consists of thin-walled elongated cells surrounding a central lacuna. The endodermis is usually well marked. A single leaf trace enters the stele directly from each leaf. In *N. flexilis* a few ringed or spiral tracheids are to be seen at the nodes, especially the younger ones, also in the pedicel of the flower, and, according to CAMPBELL, in the young leaves as well. In *N. marina*, however, I am unable to find any trace of tracheary tissue, although this species is a stouter form than *N. flexilis*. The feature to which most significance has been attached is the simple flower, consisting either of a single ovule or single anther, inclosed in a "spathe." In early stages the micro- and megasporangiate structures are scarcely distinguishable, and CAMPBELL compares them with the sporangia of Azolla. This author argues for the derivation of the monocotyledons directly from pteridophytes, especially the Isoetaceae, through simply organized aquatics such as Naias or Zannichellia. According to this view the simplicity exhibited by the vegetative and reproductive structures is primitive. In marked contrast is the opinion of MAGNUS: "Bei Naias scheint mir vieles dafür zu sprechen, das wir es mit reducirter Einfachheit zu thun haben" (**18**, p. 222). It will be well to examine the evidence in some detail.

(1) On the view that Naias represents a reduced form derived from a land plant, the occurrence of tracheids at the nodes, in the pedicels of the flowers, and in the young leaves, receives ready explanation, for these regions are just the ones in which ancestral features are apt to persist. On the other hand, there seems to be no reason why a submersed aquatic which is primitively an aquatic should have any tracheids whatever. Under this head the evidence seems conclusive.

(2) "The flowers of Naias represent the simplest form which an angiospermous flower can assume, consisting simply of a single carpel with but one ovule, or of a single stamen which in most species has but one pollen cavity" (CAMPBELL **3**, p. 12). The inaccuracy of the last statement can be easily shown. By sorting out the species described in RENDLE'S paper, it is found that seven species have a unilocular anther, while twenty-three have the usual quadrilocular anther. Moreover, CAMPBELL figures a case where the anther of *N. flexilis* is partially divided by a partition. It would seem then that *N. flexilis* forms an exception to the condition obtaining in the genus, hence the similarity between megasporangiate and microsporangiate structures is not so great as supposed. Concerning the single stamen, it by no means follows that this necessarily indicates a primitive condition, for there are cases of monandrous flowers belonging to families which are admitted to be high in the scale, for instance Hippuris and many orchids.

(3) The ovary of *N. marina* is surmounted by three stigmas (sometimes two), that of *N. microdon* by three stigmas, or by two stigmas and a spine-arm, or by intermediate conditions; other species show a varying number of stigmas (see RENDLE'S figures). The number of stigmas in a flower is usually taken to indicate the number of carpels, e. g., some grasses have two stigmas though there is only one seed. In the case of Naias, EICHLER (**10**) is of the opinion that the evidence is untrustworthy, since the stigmatic branches are of relatively late appearance. It may be, however, that we have here a relic of the condition of the flower with several carpels.

(4) Naias has unisexual flowers, monoecious or dioecious; this is not regarded as being so primitive a condition as the hermaphrodite one exhibited by members of the Potamogetonaceae.

(5) Pollination in Naias is effected by means of the water in which the plants are immersed. This mode must be considered to be derived from the anemophilous mode, for non-motile spores in the higher plants are regularly carried through the air.

On the whole it seems to me that the claim of primitive simplicity for Naias cannot be maintained. The evidence goes to show that its structure is reduced in accordance with its aquatic habit. The genus stands very much isolated, but it has been suggested by MAGNUS that its ovary might be derived from an ancestor of Zannichellia by the suppression of all the carpels but one.

Aponogetonaceae

APONOGETON FENESTRALIS

The creeping rhizome of this bizarre plant differs markedly from those found in Potamogetonaceae, being much less lacunar and having its cells loaded with starch. The vascular cylinder is poorly defined, since no endodermis is visible and the bundles are not numerous. Some of these lie at what is to be regarded as the periphery of the central cylinder, and a few others run in the medulla. Very few of these are amphivasal, and all are weak looking strands with their xylem hardly lignified. At intervals the peripheral bundles are connected by a girdle of vascular strands, so that an almost complete ring is formed. Seven or more traces enter from the sheathing base of each leaf, rapidly traversing the cortex and penetrating to near the middle of the stele, where they anastomose with one another and proceed downward through the medulla. Thus the vascular structure resembles that of the majority of monocotyledons which have a creeping rhizome much more than it does that of Potamogeton. In this respect and in its floral characters the genus seems more closely related to Alismaceae or Juncaginaceae than to the families so far discussed.

Juncaginaceae

TRIGLOCHIN MARITIMA

It is not intended to enter in any detail into the morphology of this genus, but to call attention to certain features which seem of theoretic interest. Contrary to the habit of the plants at the other end of the series, Triglochin has a stocky subterranean stem with short internodes, resembling Acorus and many of the sedges. *Fig. 33* shows its central cylinder; an endodermis is visible, within which are a number of bundles, mostly amphivasal, imbedded in fundamental tissue which is not lacunar as is the cortex, but contains much starch. In the center of the stele is an island of mechanical tissue. The presence of amphivasal bundles throughout the length of the stele easily distinguishes this genus from Potamogeton. The writer has already (6) expressed the view that such bundles arising in the nodes by reason of fusion of leaf traces with other strands may continue in their amphivasal condition from one node to another in case the internodes are short, as is the case in a stocky stem such as occurs in this genus. The leaf traces are collateral and penetrate the cortex rather rapidly to enter the central cylinder. *Fig. 27* shows a transverse section through the floral axis. The exceedingly dicotyledonous looking ring of collateral bundles cannot fail to be remarked. Attention has already been called to the persistence of ancestral features in the floral axis. and we have here a particularly good case in point.

SCHEUCHZERIA PALUSTRIS

The rhizome of this monotypic genus bears a general resemblance to that of Triglochin, but its tissues are much more lacunar, both in the intra- and extra-stelar regions. The cortex lacks the mechanical fibers found in Triglochin, and the island of such tissue is absent from the stele. Numerous leaf traces enter the cortex from the sheathing leaves; the larger traces penetrate directly into the interior of the stele, while the smaller ones run down through the cortex for nearly the length of an internode before entering the central cylinder. The structure of the central cylinder of the rhizome is shown in *fig. 34;* leaf traces are to be seen in various stages of penetration in to the cylinder. Most of the bundles lie in a circle at the outer border of the stele, and it will be noticed that practically all of them are amphivasal, although CHATIN (4) figures them as collateral. It is probable that his figure is from a higher region of the stem, for I have found that in this region the bundles are more nearly collateral, i. e., with U-shaped xylem. It is of interest to add that in the upper nodes the leaf traces enter the stele through distinct gaps. The floral axis is strengthened by a thick fibrous ring, inside which are collateral bundles arranged in an irregular ring, with three or four lying a short distance farther in. Thus the arrangement is not so simple as in Triglochin.

The affinities of this and the preceding genus seem to be with Alismaceae rather than Potamogetonaceae, hence no attempt will be made at present to discuss this question.

Relationships

The view that the monocotyledons have been derived from the dicotyledons has been put on a new foundation by recent anatomical studies. Since the correctness of this view is to be premised in the following discussion, it will be well to review the evidence for it. The two characteristic monocotyledonous features—scattered arrangement of the bundles and amphivasal form of bundle—are found not to occur in the seedling in families which have been examined in this respect (JEFFREY **13**, CHRYSLER **5**, PLOWMAN **19**). On the contrary, the seedling shows a tubular stele with collateral bundles, such as is typical of a dicotyledon. Sooner or later some of the bundles turn into the medulla and show the amphivasal feature at some part of their course, eventually becoming leaf traces. These stages in ontogeny are believed to repeat stages in the phylogeny of the group. Occasional cases of apparent reversion to the primitive type occur in adult rhizomes, such as that of Clintonia. The tubular stele is found in the floral axis of some monocotyledons, and its occurrence here has been interpreted as the persistence of an ancestral feature. In this organ and in the leaves, moreover, only collateral bundles are found, which is the prevailing type in dicotyledons. A cambium, the lack of which was supposed to be a distinguishing feature of monocotyledons, has been demonstrated in Gloriosa by QUEVA (**20**), in the seedlings of a number of monocotyledons by ANDERSSON (**1**), in Cyperaceae by PLOWMAN (**19**), and most recently in the nodes of grasses by the present writer (**6**). It has been argued that in the last-mentioned case the cambium has persisted in regions where it is of use, and is therefore a vestigial not a rudimentary structure. As to geological evidence, many of the supposedly ancient monocotyledons have turned out to be gymnosperms, and there is no reason for believing that monocotyledons existed earlier than dicotyledons. Finally the researches of Miss SARGANT have shown how a monocotyledonous embryc may have been derived from a dicotyledonous one.

The present research has added to the evidence along at least one of the lines just mentioned. It has been shown that in Triglochin and various species of Potamogeton the floral axis contains a circle of collateral bundles, in which respect it is sharply distinguished from the leafy shoot, especially in Triglochin. It has also been pointed out that in the creeping stem of Potamogeton, where no large leaves send in traces, the central cylinder has a simple tubular form, though this appearance is often masked by the large size of the dorsal and the ventral strand. In the elongated internodes of Potamogeton only collateral bundles occur, while in the shortened axis of Triglochin, to which many leaves are attached, amphivasal bundles are numerous. This apparently represents the direction of evolution. Lack of material has so far prevented me from studying the seedlings of any of the Helobiae, but the importance of such study is fully recognized, and cultures are in progress which it is hoped will shortly render it possible to fill this gap in the evidence.

Admitting then the derivation of the monocotyledons from dicotyledon-like ancestors, which of the genera studied most closely resemble the dicotyledons? There seems to be sufficient reason for considering Potamogeton the most primitive genus met with, as is indicated by the following facts:

(1) The stem of Potamogeton is not a shortened axis, such as is seen in many of the monocotyledons, e. g., the rhizome of Triglochin, which in all probability has been shortened and thickened in accordance with its geophilous habit.

(2) Xylem is well developed in the nodes, floral axis, and young stem of many species of Potamogeton. Its presence in these regions cannot be explained on physiological grounds, but must be regarded as the persistence of an ancestral feature. Conduction must be performed by the internodes as well as the nodes, therefore if the tracheary tissue were functional (i. e., rudimentary instead of vestigial) in the immersed species, its occurrence ought not to be localized.

(3) The separate strands present in the central cylinder of such species as *P. pulcher* are to be regarded as more primitive than the compound or fused cylinder seen in Zostera, etc.

(4) Potamogeton shows the circle of bundles in the floral axis more plainly than any other genus studied, with the exception of Triglochin. The significance of this feature has already been considered.

(5) The phloem in Potamogeton is particularly well developed, consisting of sieve tubes with evident sieve plates, and undoubted companion cells, though the latter are seldom so plain in monocotyledons as in dicotyledons.

(6) Some species of Potamogeton possess floating leaves. Though it is not denied that this may be a specialized feature, it has been well

argued by SCHENCK (27) that we have here a stage in the assumption of aquatic life by the genus. The leaves of all the other members of the family are submersed.

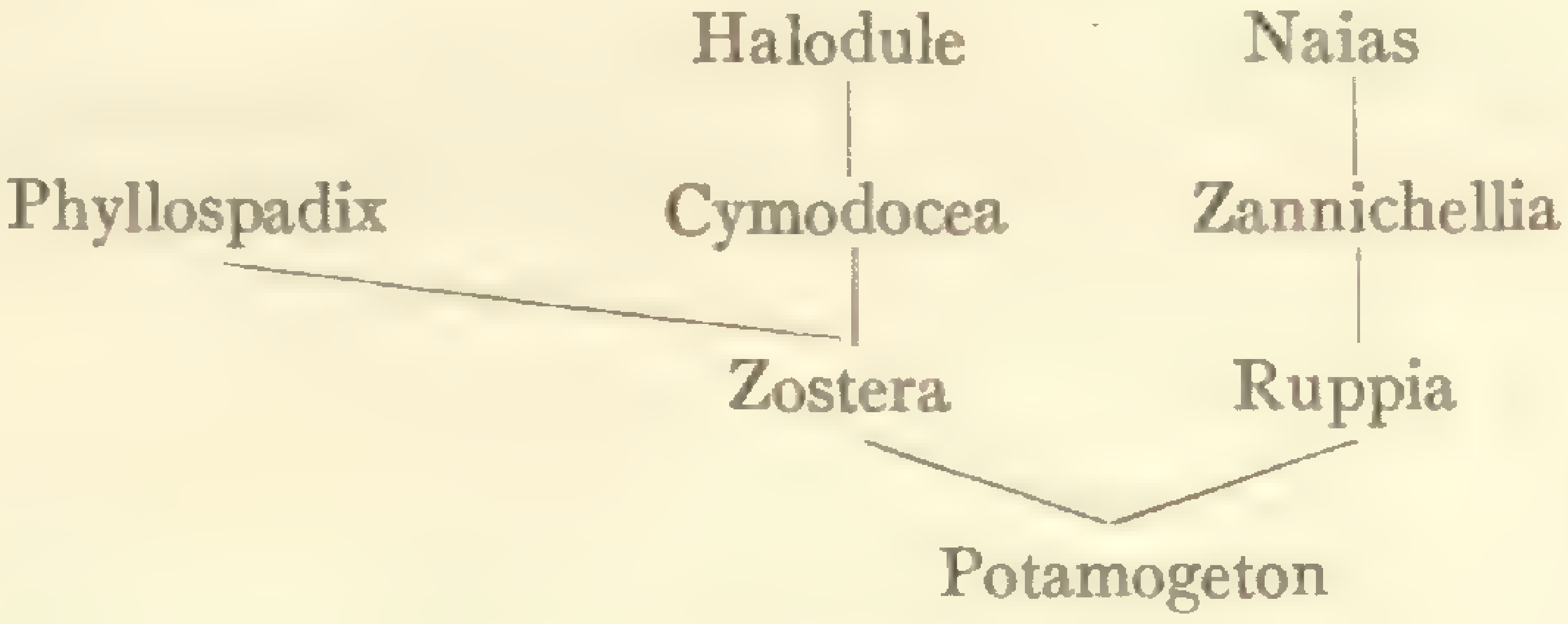
(7) The inflorescence is a spike or spadix, an admittedly primitive form. The other genera show a specialized spadix, such as Zostera, or a reduced inflorescence, as in Zannichellia (and Naias).

(8) The spadix in Potamogeton is raised above the surface of the water so that pollination is anemophilous. The nearest approach to this is in Ruppia, where the pollen floats on the surface of the water, while in the other genera the inflorescence is submersed and the pollen does not reach the surface. In connection with this habit the pollen of Zostera and Cymodocea is filamentous. Evidently these cases of hydrophilous pollination are adaptations.

(9) The floral parts are in whorls of four, which is a characteristic dicotyledonous number, although the whorls do not alternate in the simplest way. There is only slight coalescence of parts.

(10) The flowers are perfect, while in Zannichellia and Naias they are monoecious or dioecious.

As to the relationships among the genera, the tendency of recent classifications is indicated by the fact that the old family Naiadaceae is now split into four families, and one of these (the Potamogetonaceae) into five not very closely related sections. It appears that the leading principle at work in the evolution of the families has been that of simplification or reduction, both in the reproductive and the vegetative organs. Some features of specialization and complexity have also appeared, such as the filamentous pollen and flattened spadix of Zostera. This genus in spite of its peculiarities seems to stand more closely related to Potamogeton than to the reduced genera Ruppia, Zannichellia, and Naias, and its vascular system at least may be derived from that of Potamogeton, as has already been shown. The vascular system of Ruppia may represent a reduced condition derived from that of Zostera or Potamogeton, while Zannichellia and Naias are still more reduced both as regards the vascular system as a whole and the elements of which it is composed. Naias represents the extreme of reduction found in the group, for there is a single leaf trace, and tracheary tissue is found only in certain species, such as *N. flexilis*, and is confined to a few scattered tracheids at the nodes, the pedicel of the flower, and the young leaves. In contrast to this simplification, the genus Zostera leads to a state of greater complexity in Cymodocea and Halodule, where the two cortical strands of *Z. marina* are replaced by two arc-shaped groups, each of several strands but with a similar relation to the leaf traces and central cylinder. Phyllospadix differs so little from Zostera in its vascular tissues, that if this were the only criterion both might be included in the same genus. Triglochin and Scheuchzeria appear to be only remotely related to the foregoing genera. Both are much more typical monocotyledons, as appears from the rhizome and flowers, and are more naturally related to the Alismaceae. Aponogeton seems to be more closely related to Alismaceae and Juncaginaceae than to Potamogetonaceae. The following diagram represents in a graphic way certain of the relations suggested in the foregoing account:



Summary

1. The course of the leaf traces in Potamogeton is not typically monocotyledonous, for in the more robust species the three traces run down through one internode at the periphery of the central cylinder before entering the medulla, where they descend through a second internode, finally fusing with cauline strands.

2. At the points of fusion the bundles are found to be amphivasal, while they are collateral throughout their internodal course.

3. The phloem of the bundles at the base of a branch shows a marked swelling.

4. The cortical bundles present in some species of Potamogeton are not regarded as a primitive feature, since they do not occur in the fertile part of the floral axis and occur only sparingly if at all in the creeping stem. They enter the stem as small strands from the stipules and petioles and are not as a rule connected with the principal leaf

traces. In Zostera and Cymodocea, however, there is a system of cortical bundles which are connected with all of the principal leaf traces except the median one.

5. The circle of collateral bundles found in the floral axis in Potamogeton and Triglochin is regarded as a relic of the ancestral dicotyledonous condition of the vascular system.

6. The evidence afforded by the vascular and floral structures indicates that Potamogeton is the most primitive genus of Potamogetonaceae. It shows more clearly than the other genera features characteristic of terrestrial life, though some of its species are apparently reduced forms.

7. Species of Potamogeton having both floating and submersed leaves and a central cylinder in which the bundles run separated from one another are regarded as the most primitive members of the genus. *P. pulcher* fulfils these requirements.

8. The other genera of Potamogetonaceae show further stages of reduction in accordance with their totally submersed habit. Their relationships are in some cases shown by the vascular structures.

9. In Naiadaceae the reduction is carried to such an extreme of simplicity that the affinities of the family are obscure.

10. Aponogetonaceae and Juncaginaceae are more typically monocotyledonous in their structure, and do not seem immediately related to Potamogetonaceae.

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EXPLANATION OF PLATES XIV–XVIII

PLATE XIV

Diagrams to show the course of the leaf traces in the different genera. In each diagram the upper part represents a transverse section through the node, and the lower part a longitudinal section through a node and part of the internode below it. The boundary of the central cylinder is indicated by broken lines, the median leaf trace by a double line, and the lateral leaf traces by single lines. In the vertical diagrams the median trace is represented for the sake of clearness as if entering from one side.

FIG. 4. Potamogeton (most species).—FIG. 5. *Potamogeton Nuttallii.*—FIG. 6. *Zostera marina.*—FIG. 7. *Phyllospadix Scouleri.*—FIG. 8. *Cymodocea manatorum.*—FIG. 9. *Ruppia maritima.*—FIG. 10. Zannichellia and Naias.

PLATE XV

FIG. 11. *Potamageton natans.* Transverse section a little above an upper node of the leafy shoot, showing the petiole, fused stipules, axillary bud, and stem. ×15.

FIG. 12. Same. Longitudinal section throngh an upper node, showing the swellings at the origin of leaf and branch bundles. ×20.

FIG. 13. Same. Part of *fig. 11* more magnified; numerous cortical bundles are visible. ×20.

FIG. 14. Same. Central cylinder of *fig. 13* more magnified. ×45.

FIG. 15. Same. Transverse section through the central cylinder at a node of the leafy shoot. ×35.

FIG. 16. Same. Transverse section through internode of the creeping stem; cortical bundles are absent. ×35.

PLATE XVI

FIG. 17. *P. pulcher.* Transverse section through central cylinder of the creeping stem at the origin of a branch. ×20.

FIG. 18. *P. pectinatus.* Transverse section through the leafy stem a short distance above a node. ×55.

FIG. 19. *P. pulcher.* Transverse section through the leafy stem just above a node, showing the absence of cortical strands characteristic of this species. ×20.

FIG. 20. Same. Central cylinder of *fig. 19* enlarged, showing the separated bundles. ×70.

FIG. 21. Same. Transverse section through an internode of the creeping stem, showing the tubular central cylinder. ×20.

FIG. 22. Same. Central cylinder of preceding figure. ×80.

PLATE XVII

FIG. 23. *P. natans.* Transverse section through fertile part of the floral axis, showing a ring of bundles. ×35.

FIG. 24. Same. Condition sometimes found in the floral axis. ×55.

FIG. 25. Same. Section from near the base of the peduncle, showing cortical bundles outside the ring. ×20.

FIG. 26. *P. hybridus.* Section through the floral axis. ×120.

FIG. 27. *Triglochin maritima.* Transverse section through the floral axis, showing a ring of collateral bundles. ×25.

FIG. 28. *P. crispus.* Transverse section through central cylinder. ×100.

PLATE XVIII

FIG. 29. *Zostera marina.* Transverse section through an internode of the ascending stem. ×20.

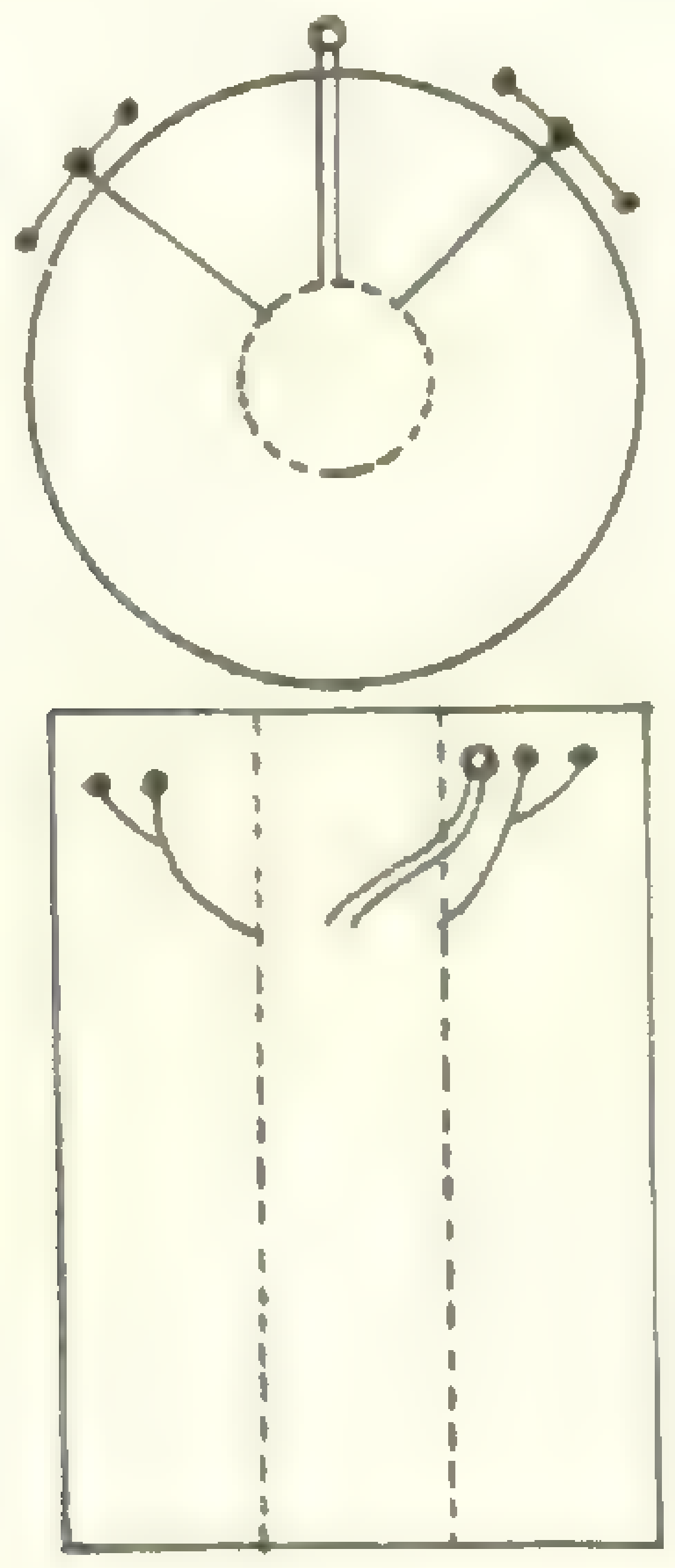
FIG. 30. *Phyllospadix Scouleri.* Transverse section through the ascending stem at the upper part of the insertion of a leaf. ×15.

FIG. 31. *Cymodocea manatorum.* Transverse section through an internode of the stem. ×25.

FIG. 32. Same. Transverse section through a node. ×30.

FIG. 33. *Triglochin maritima.* Transverse section through the central cylinder of the rhizome. ×25.

FIG. 34. *Scheuchzeria palustris.* Transverse section through central cylinder of the rhizome. ×30.



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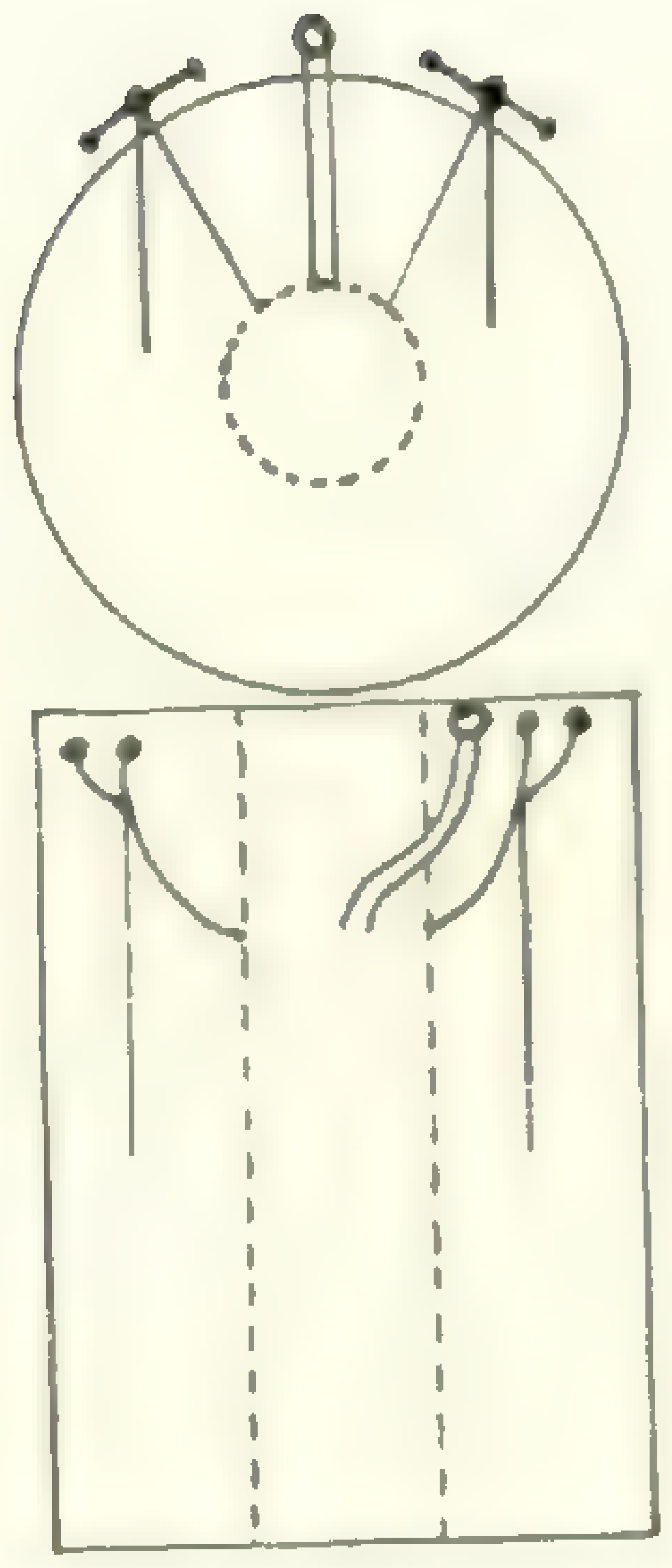

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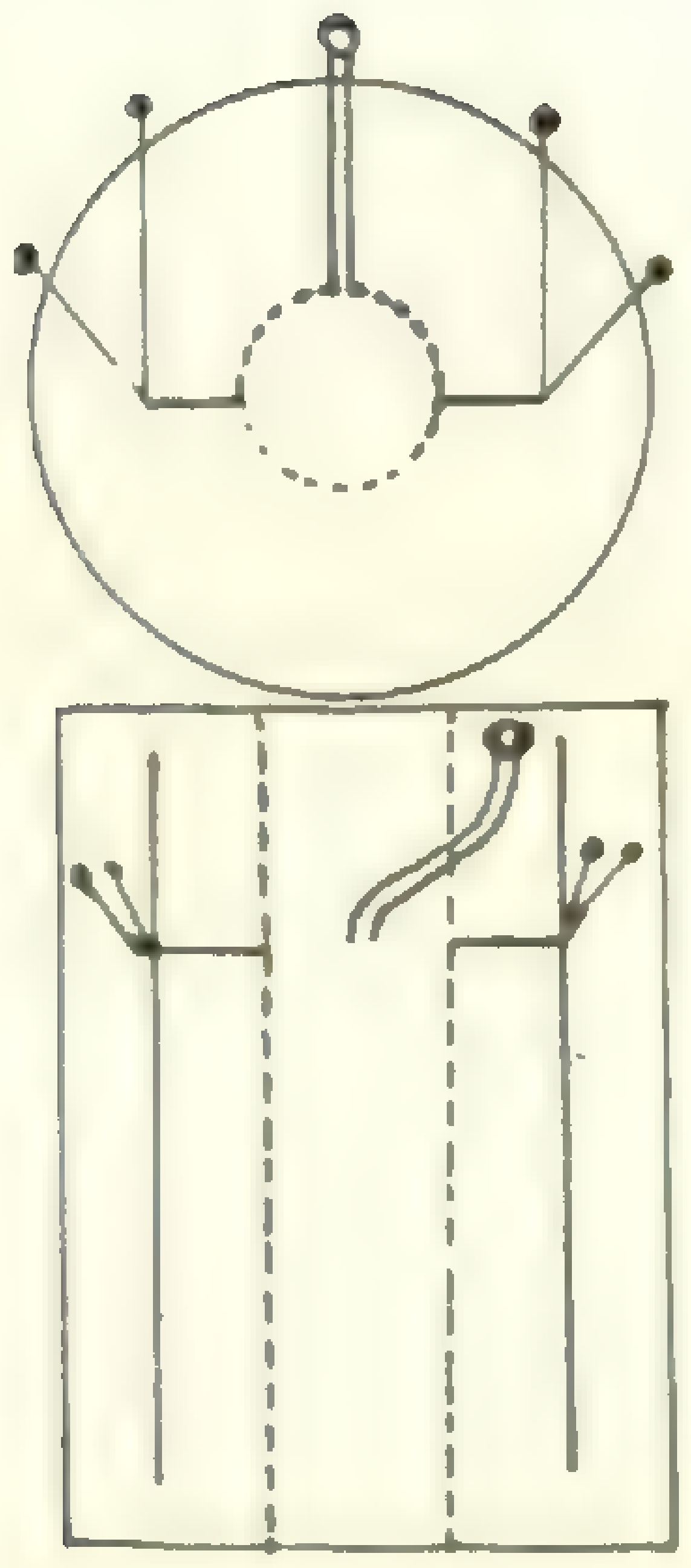

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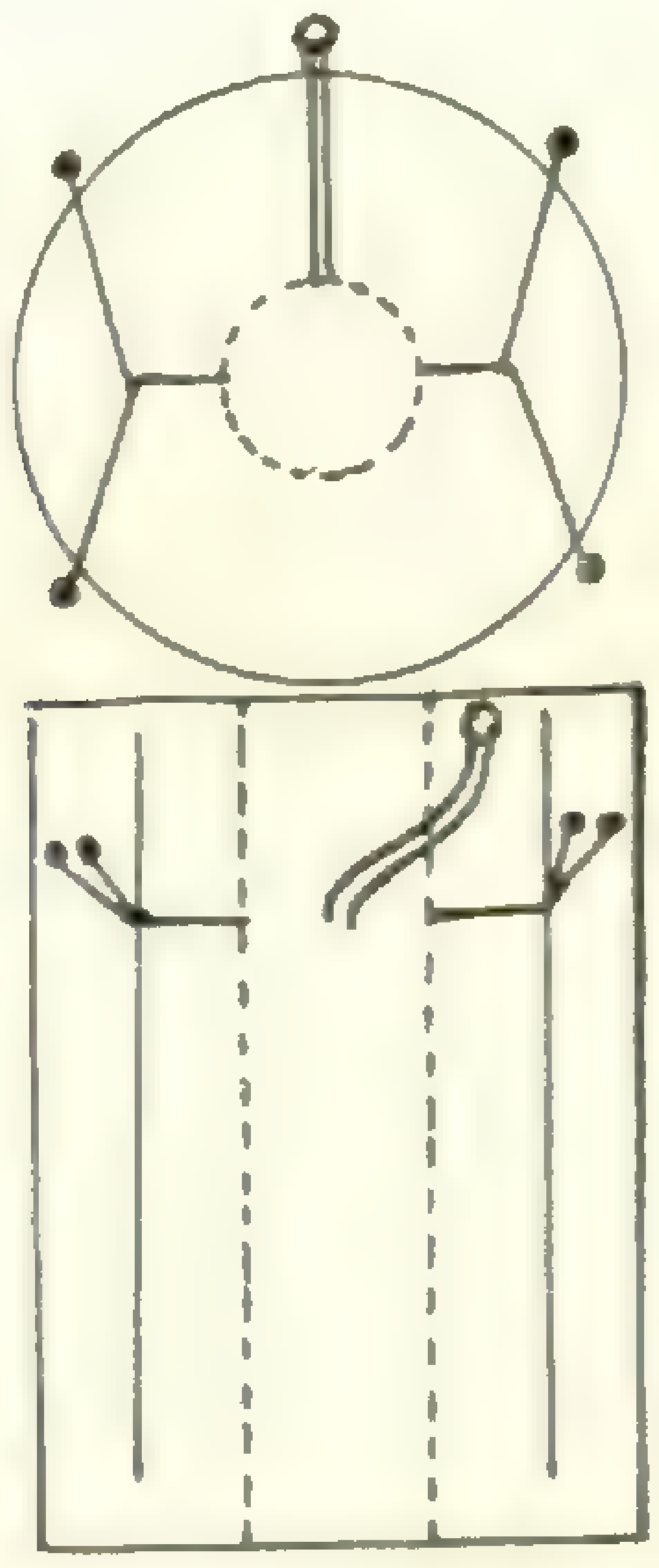

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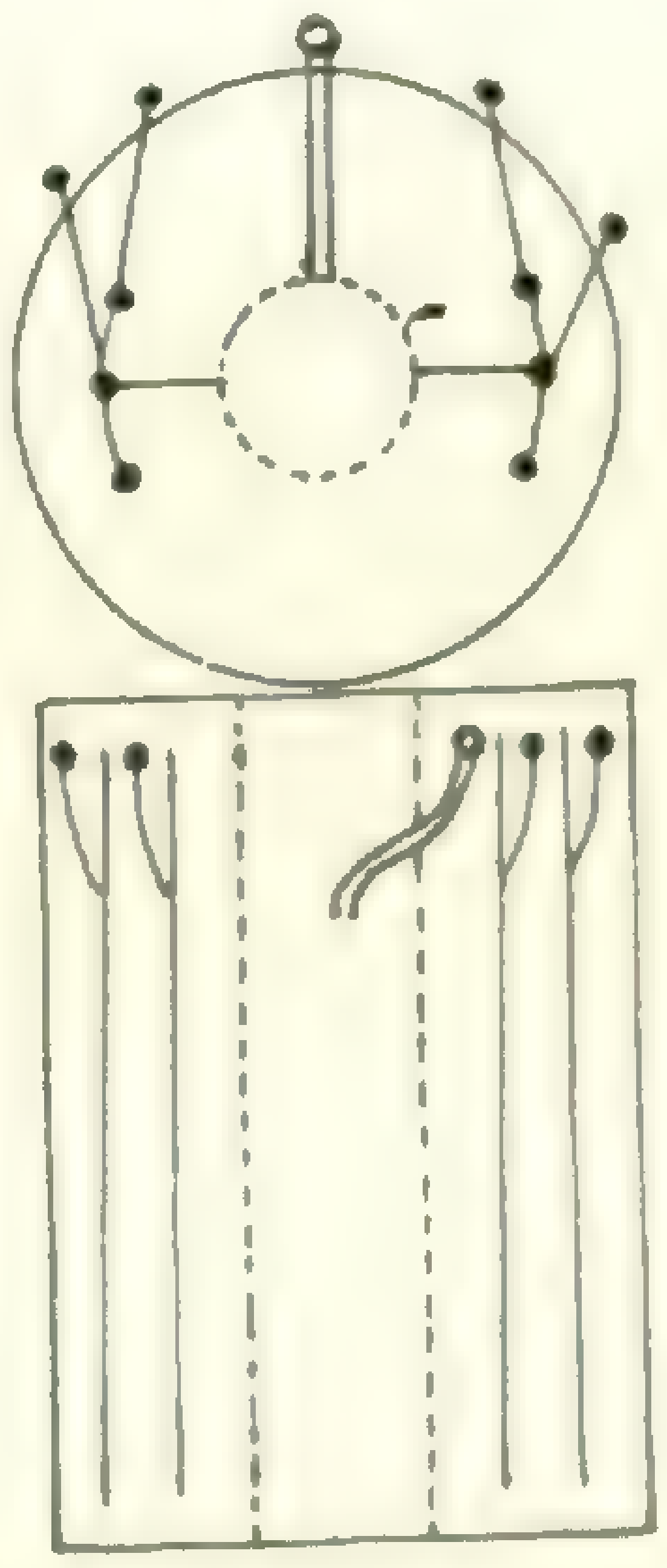

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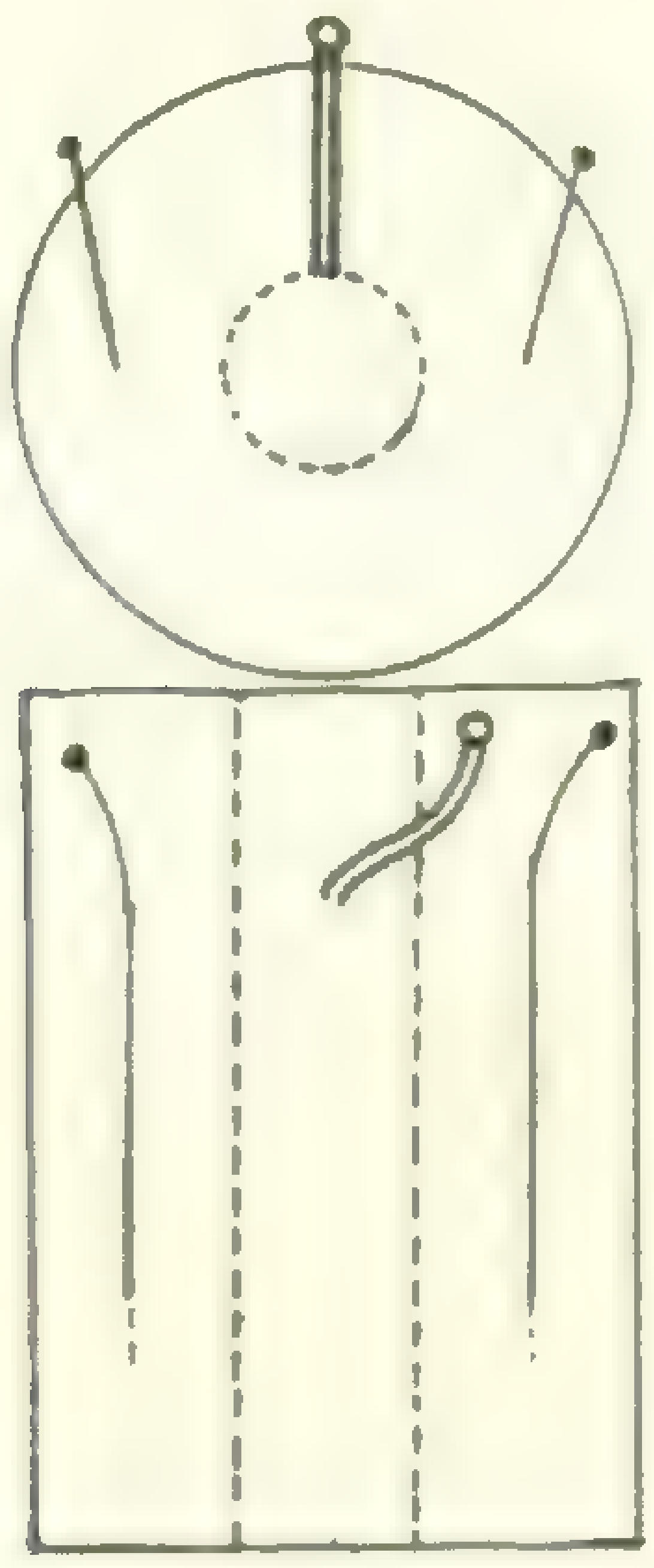

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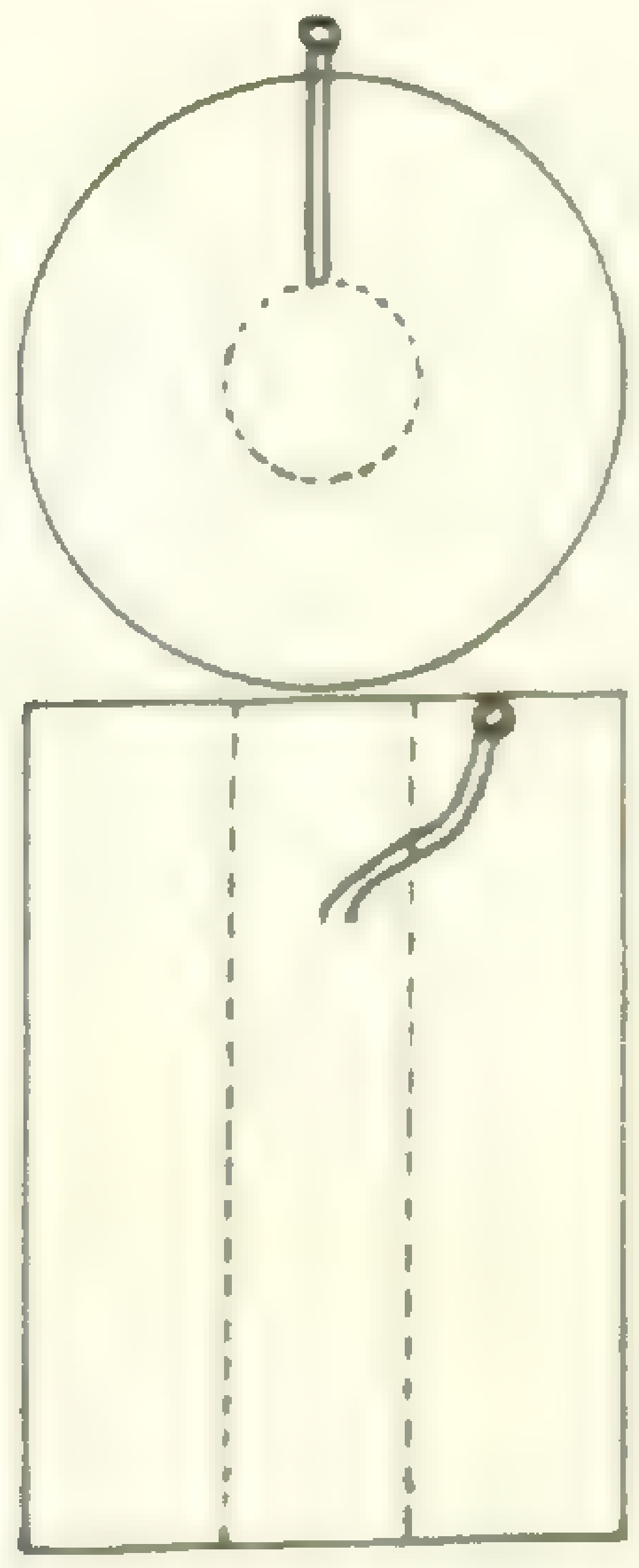

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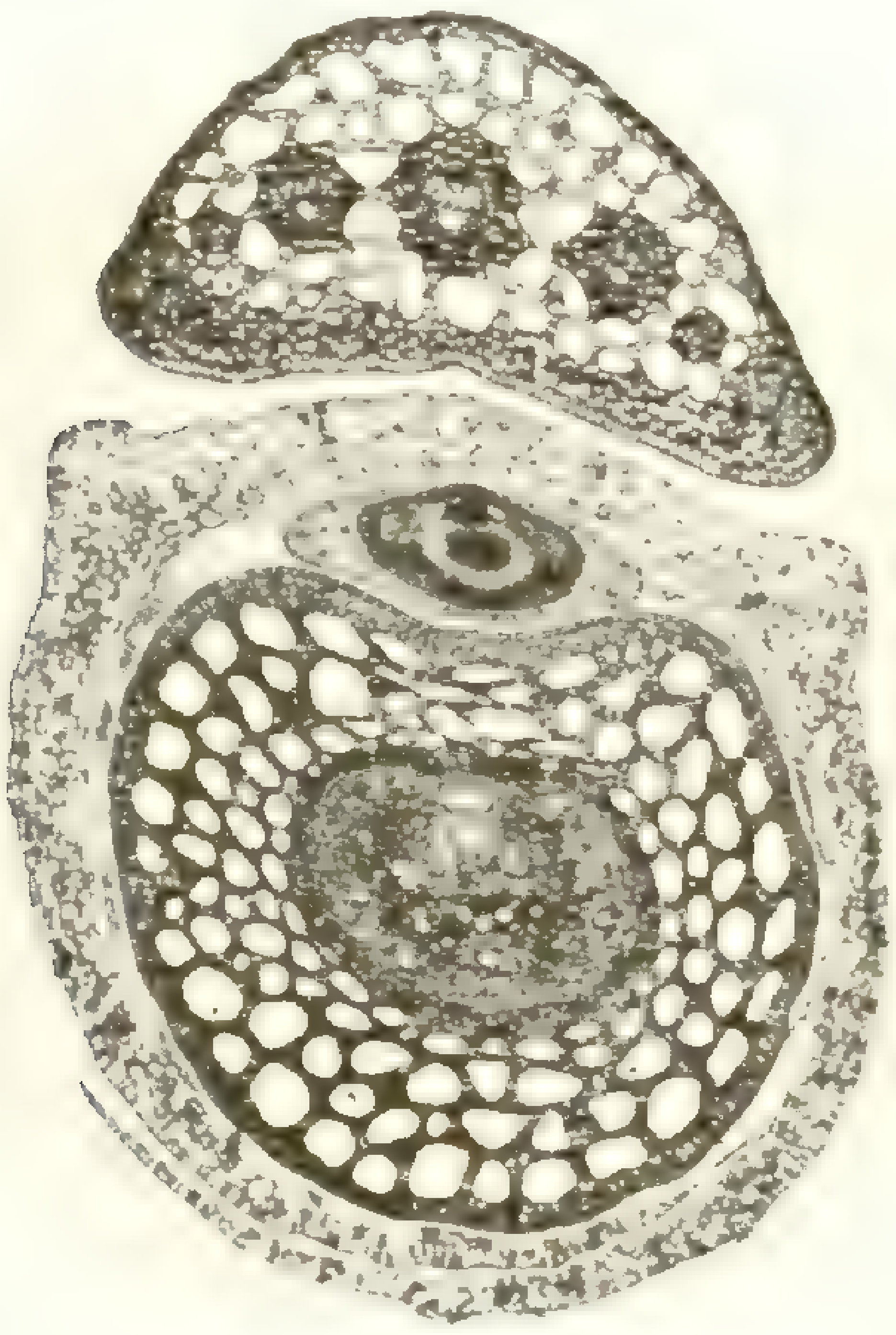
CHRYSLER on POTAMOGETONACEAE



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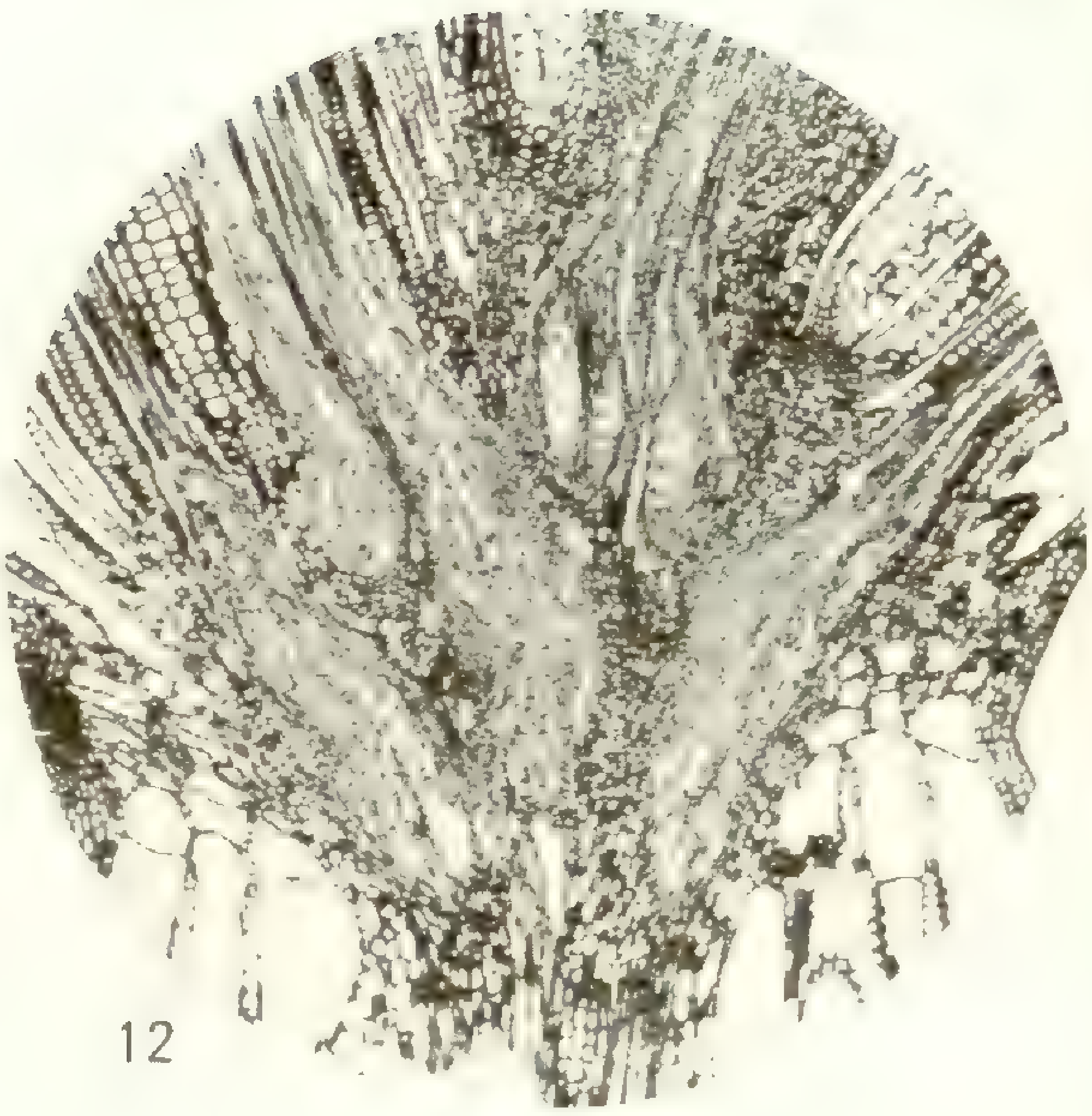

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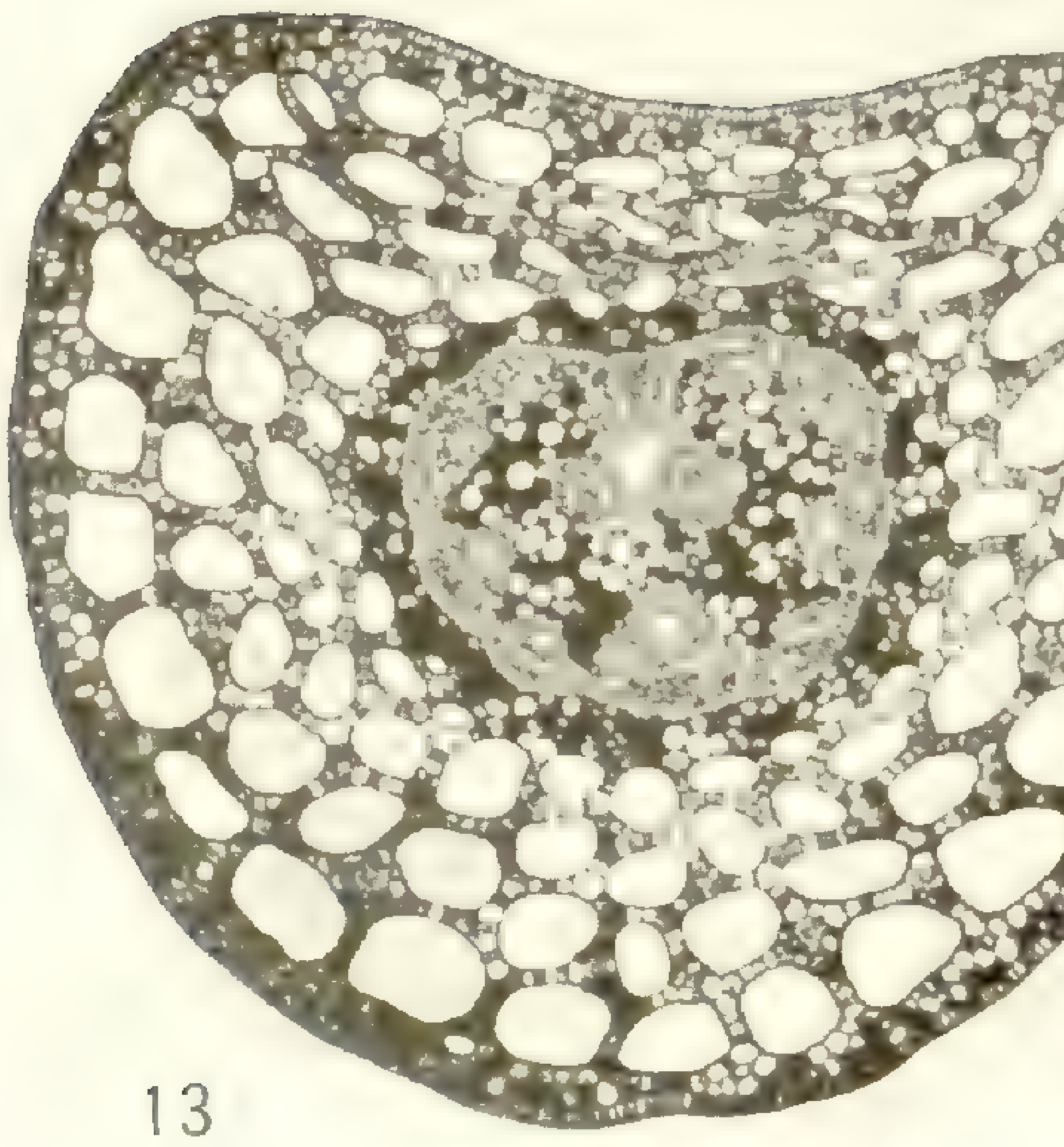

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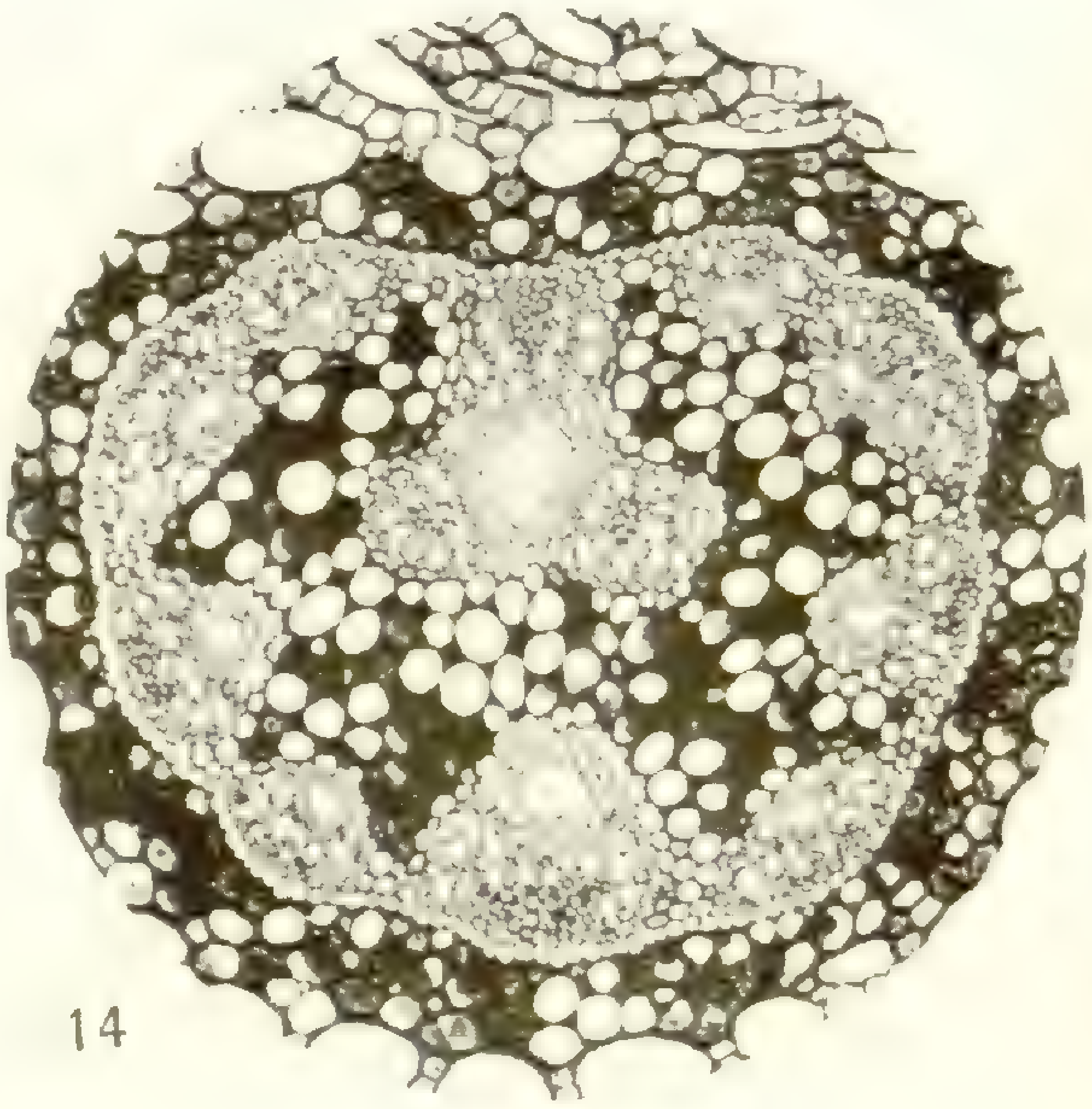

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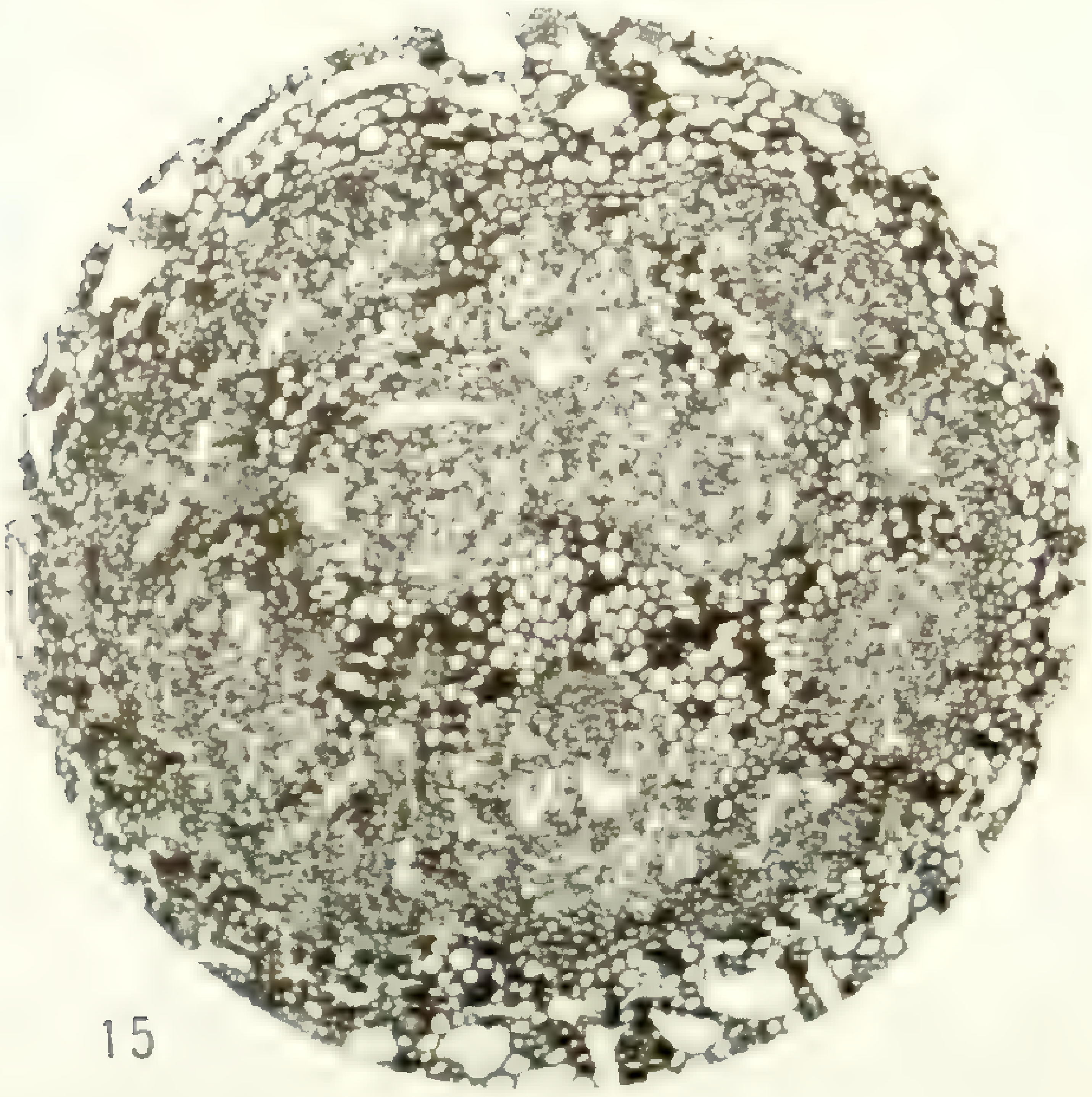

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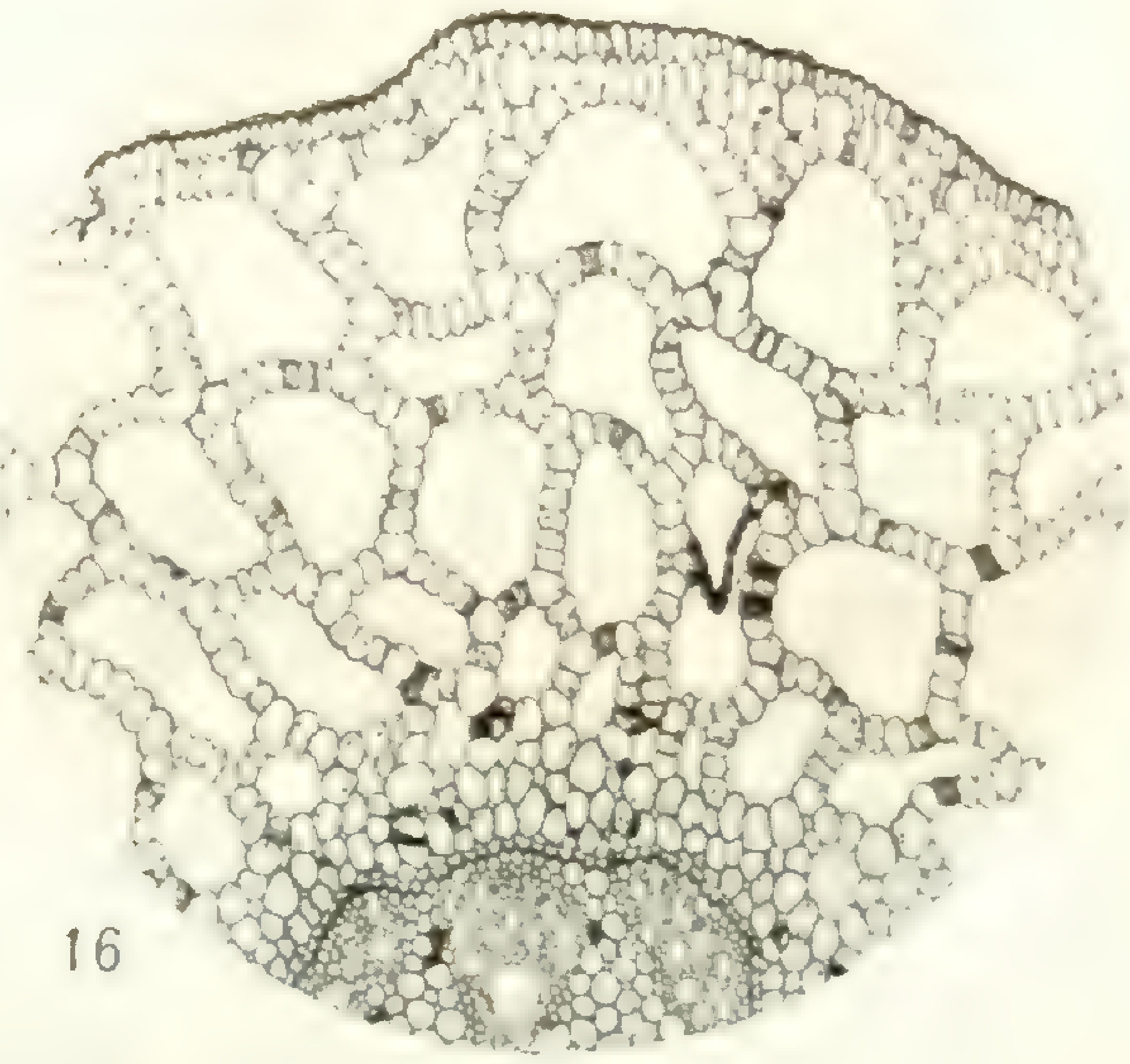

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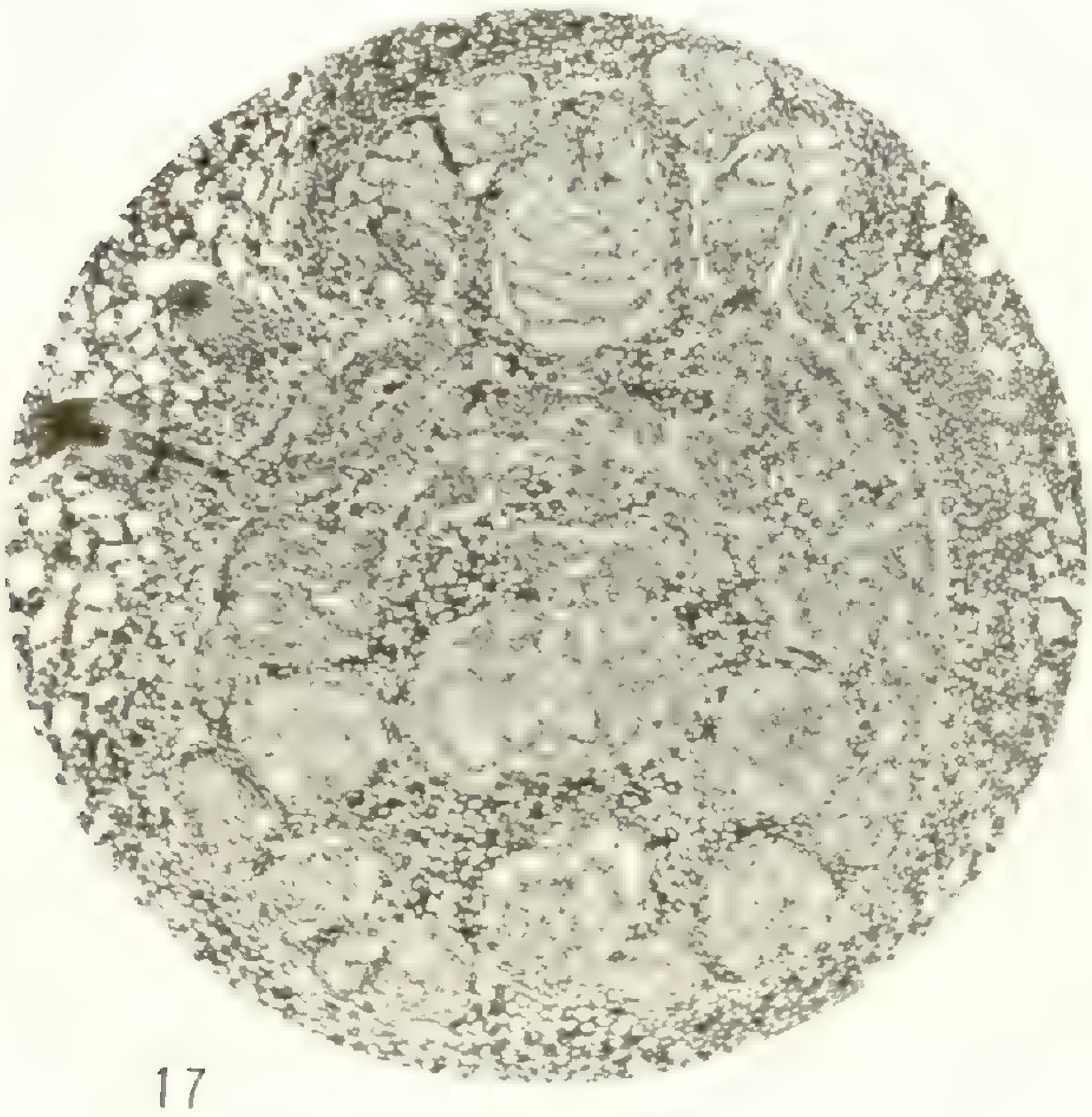
CHRYSLER on POTAMOGETONACEAE



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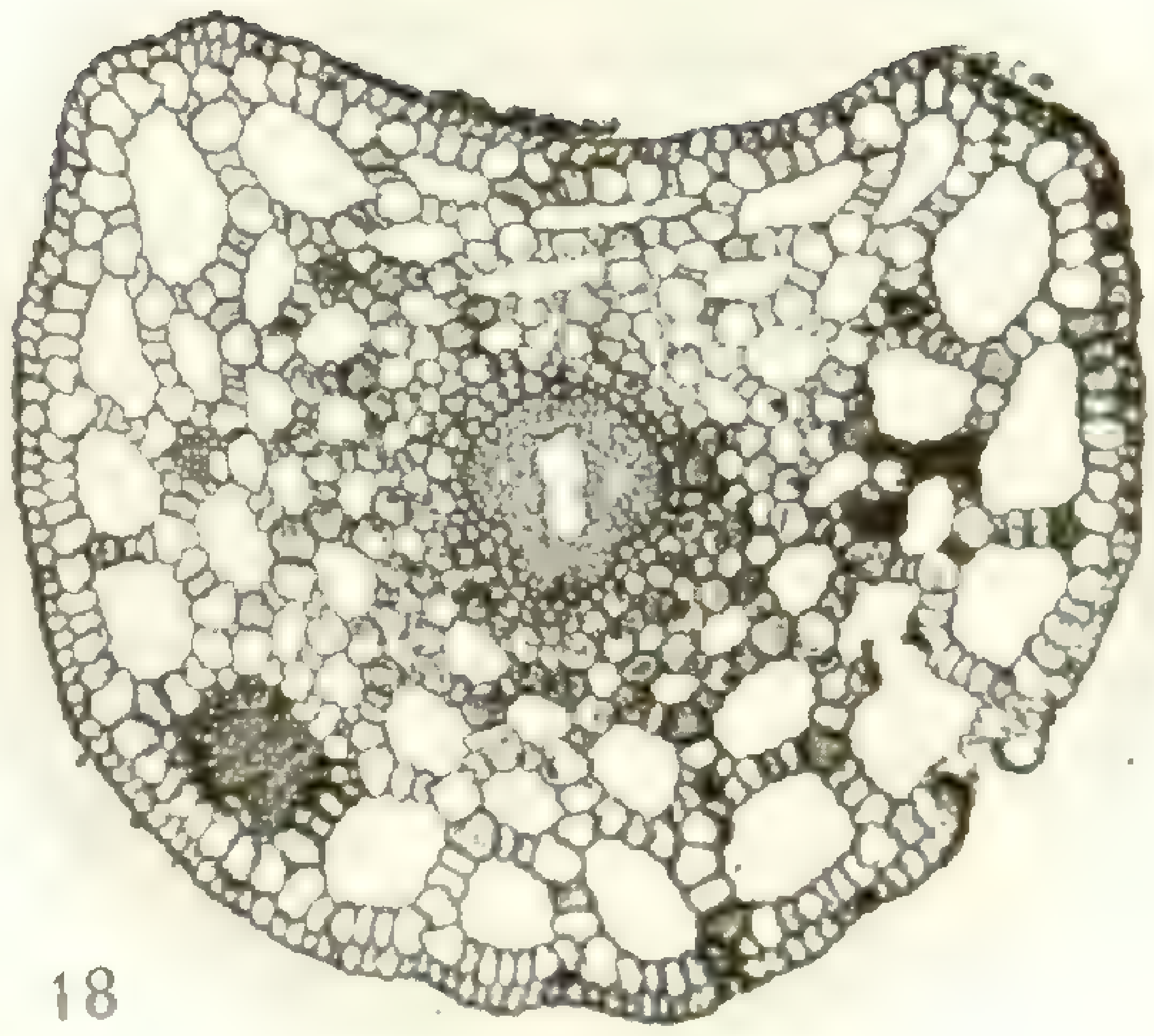

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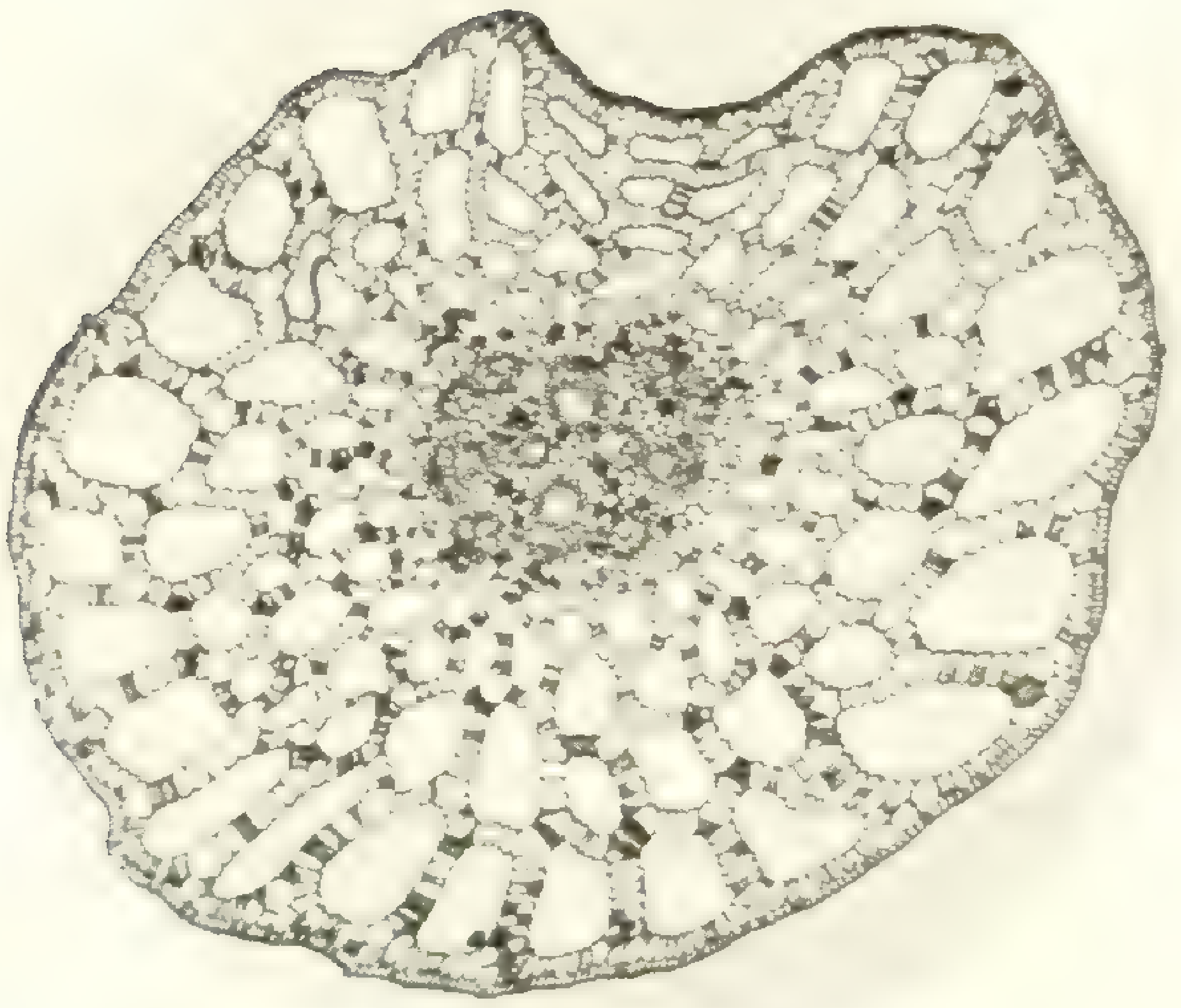

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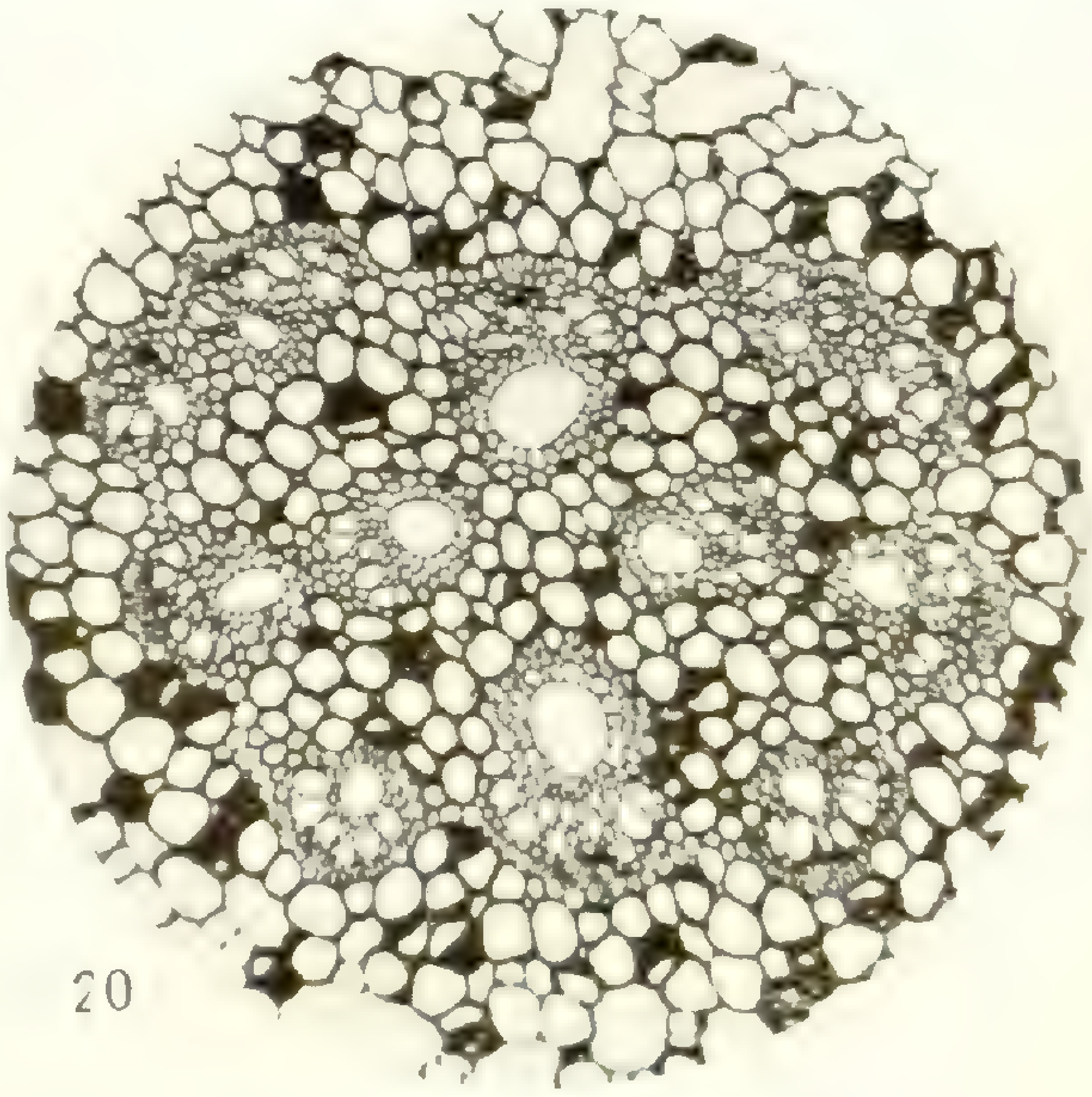

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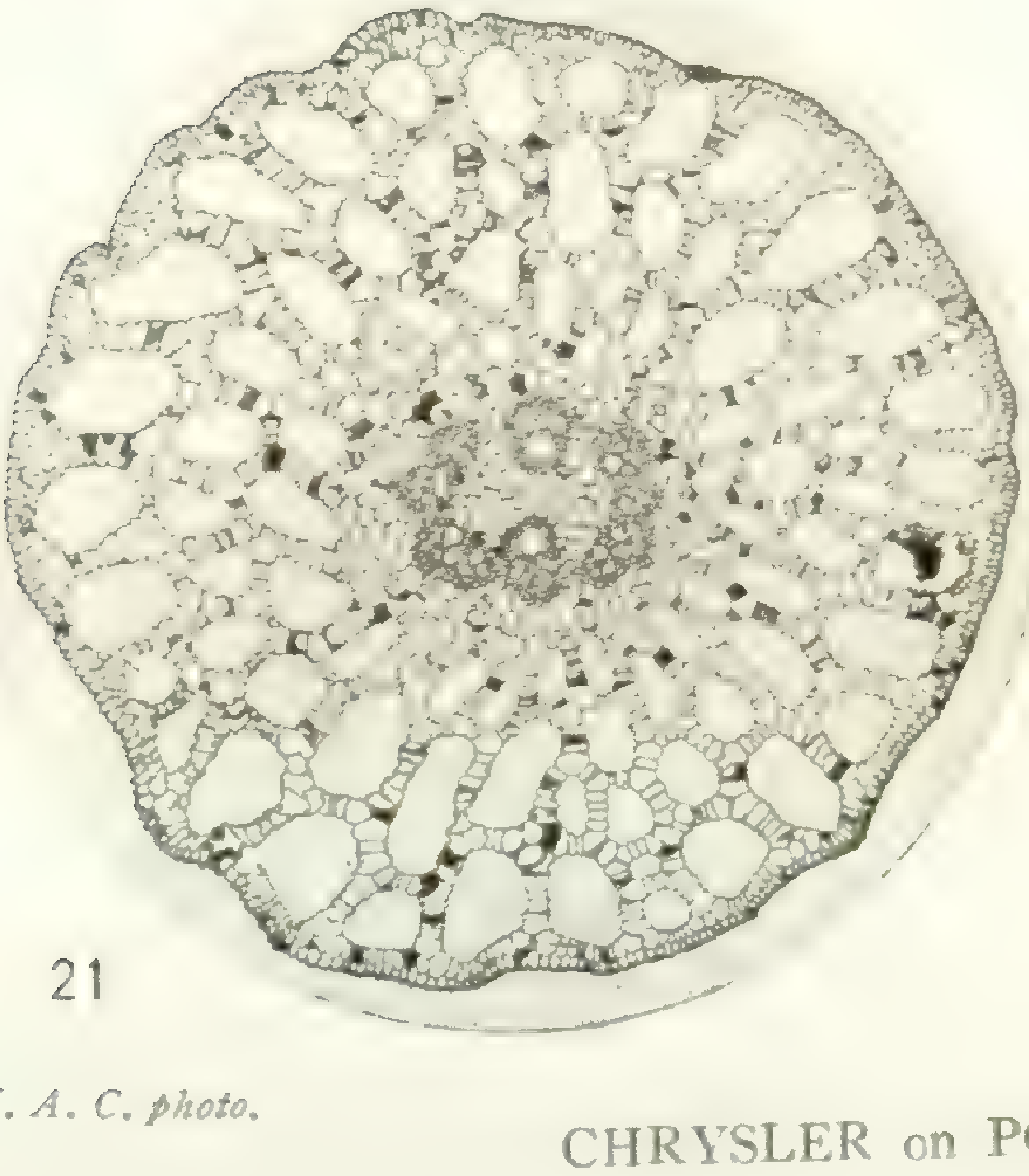

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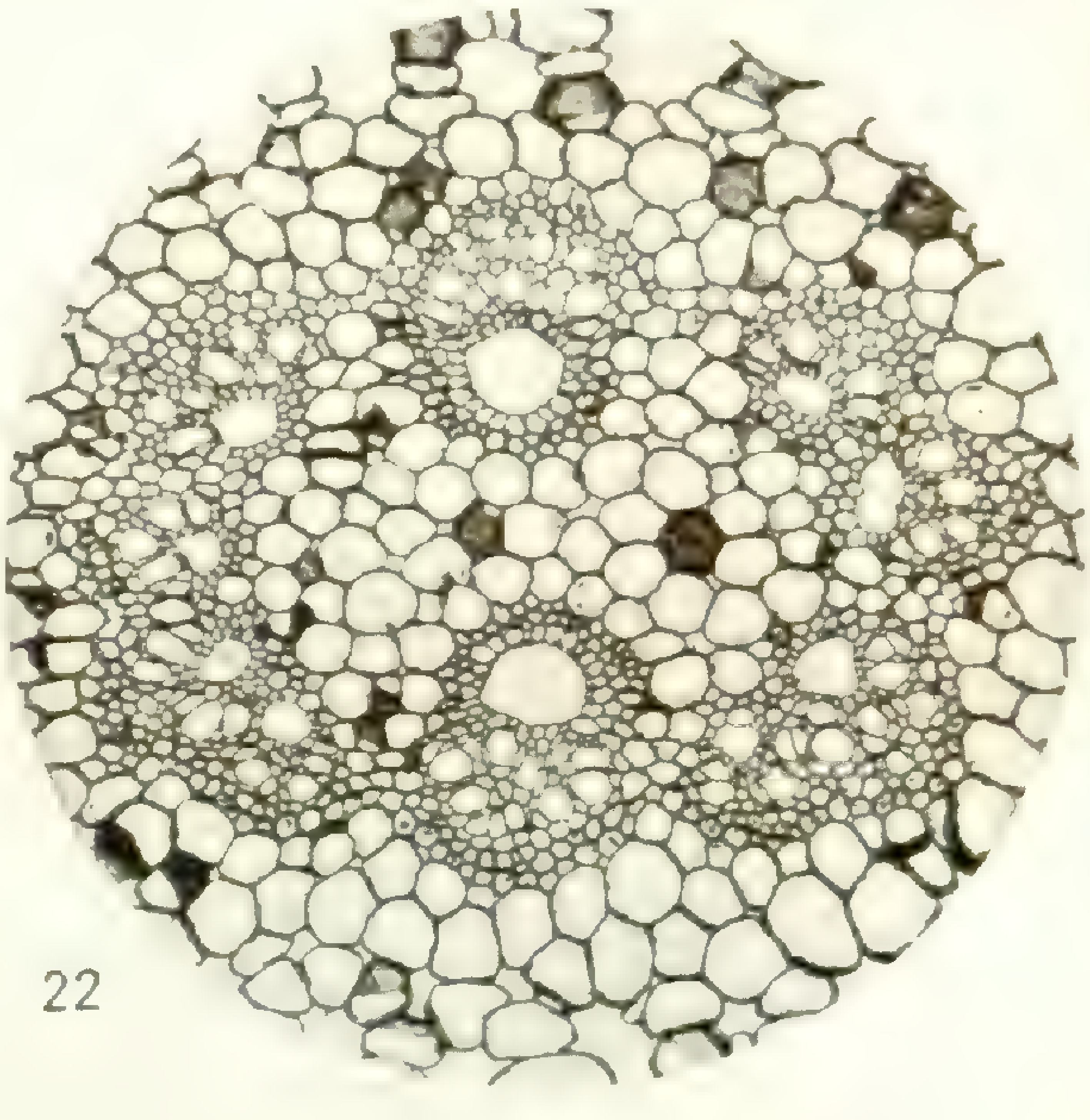

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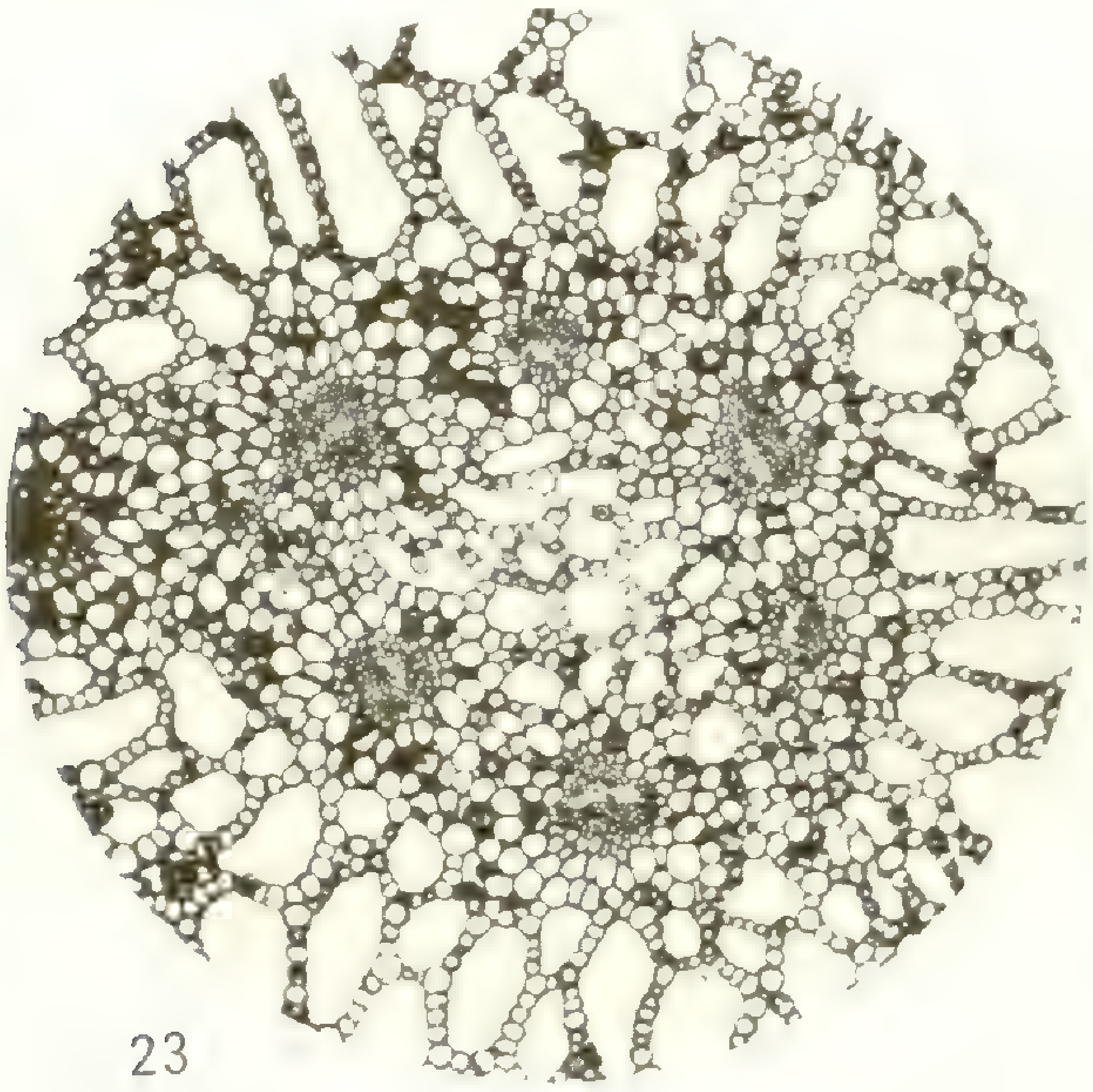

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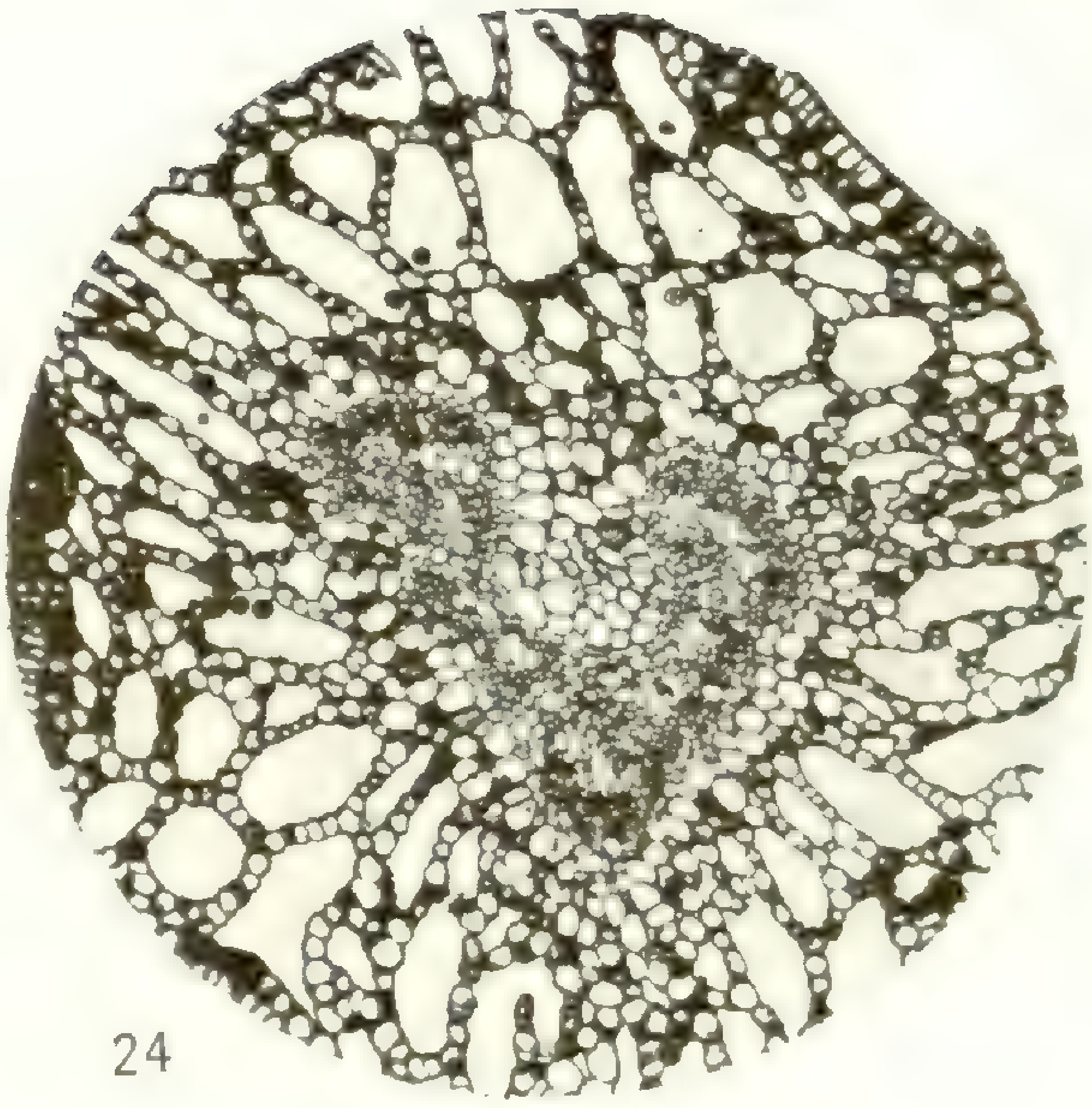

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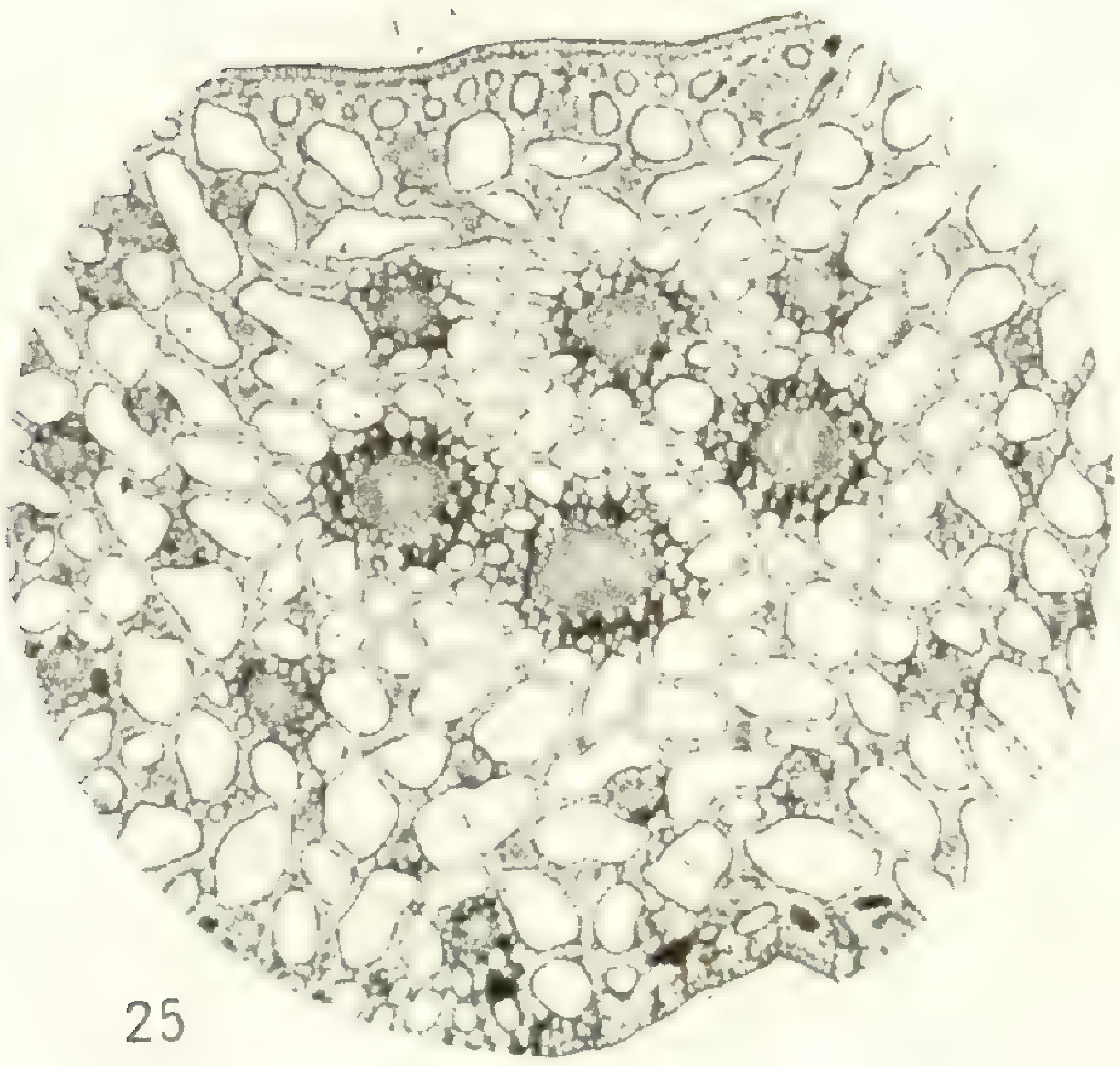

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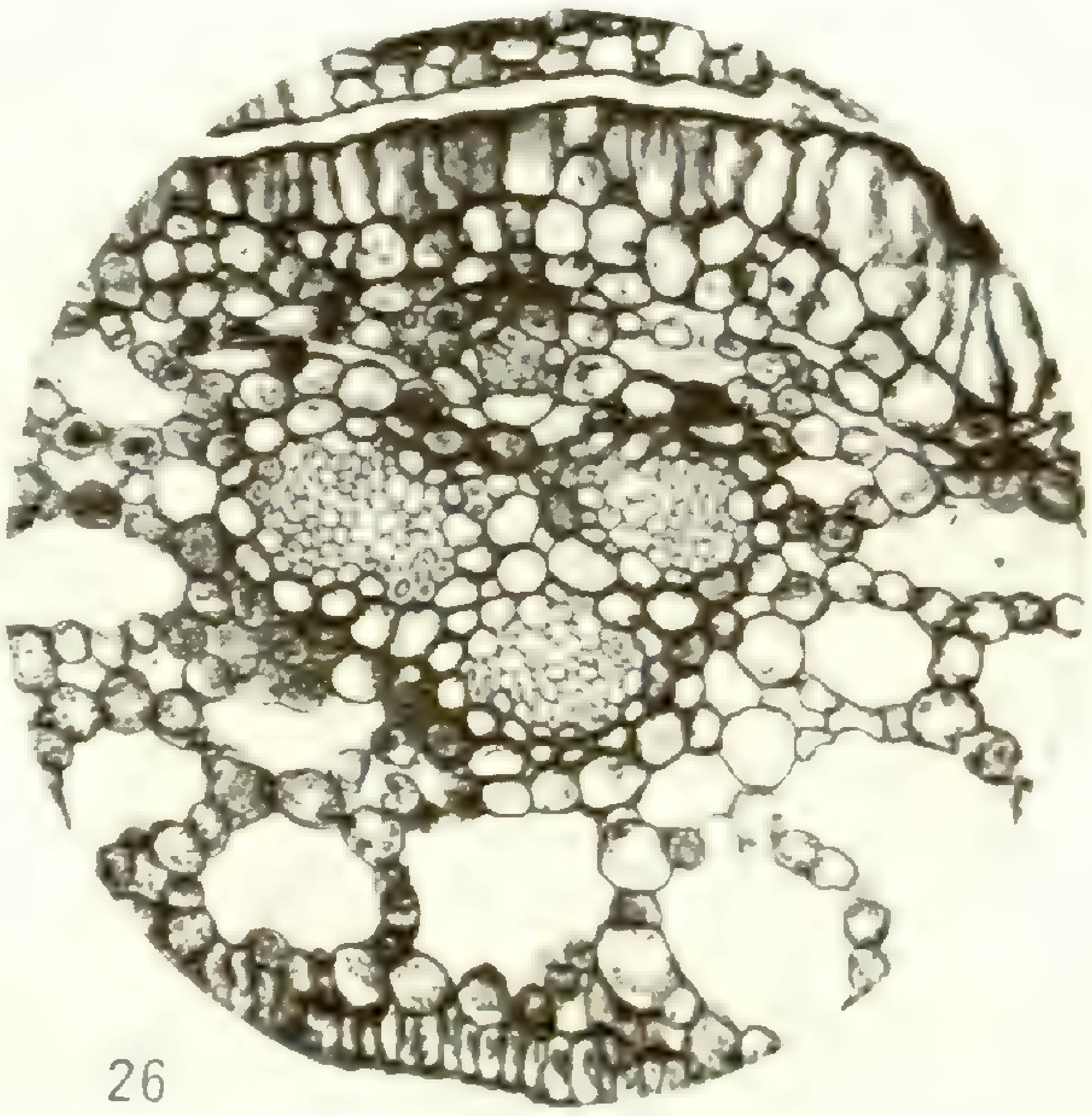

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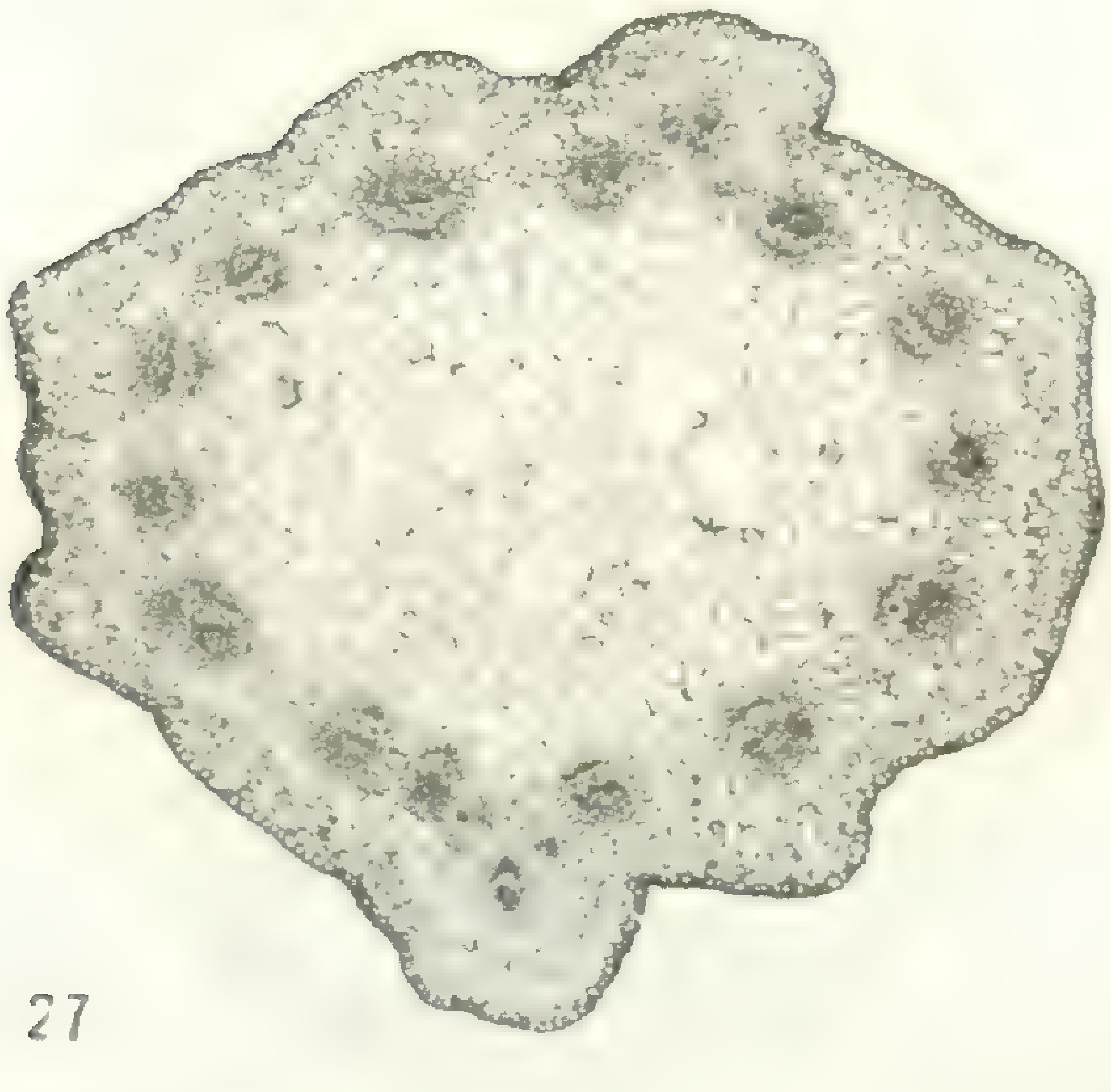

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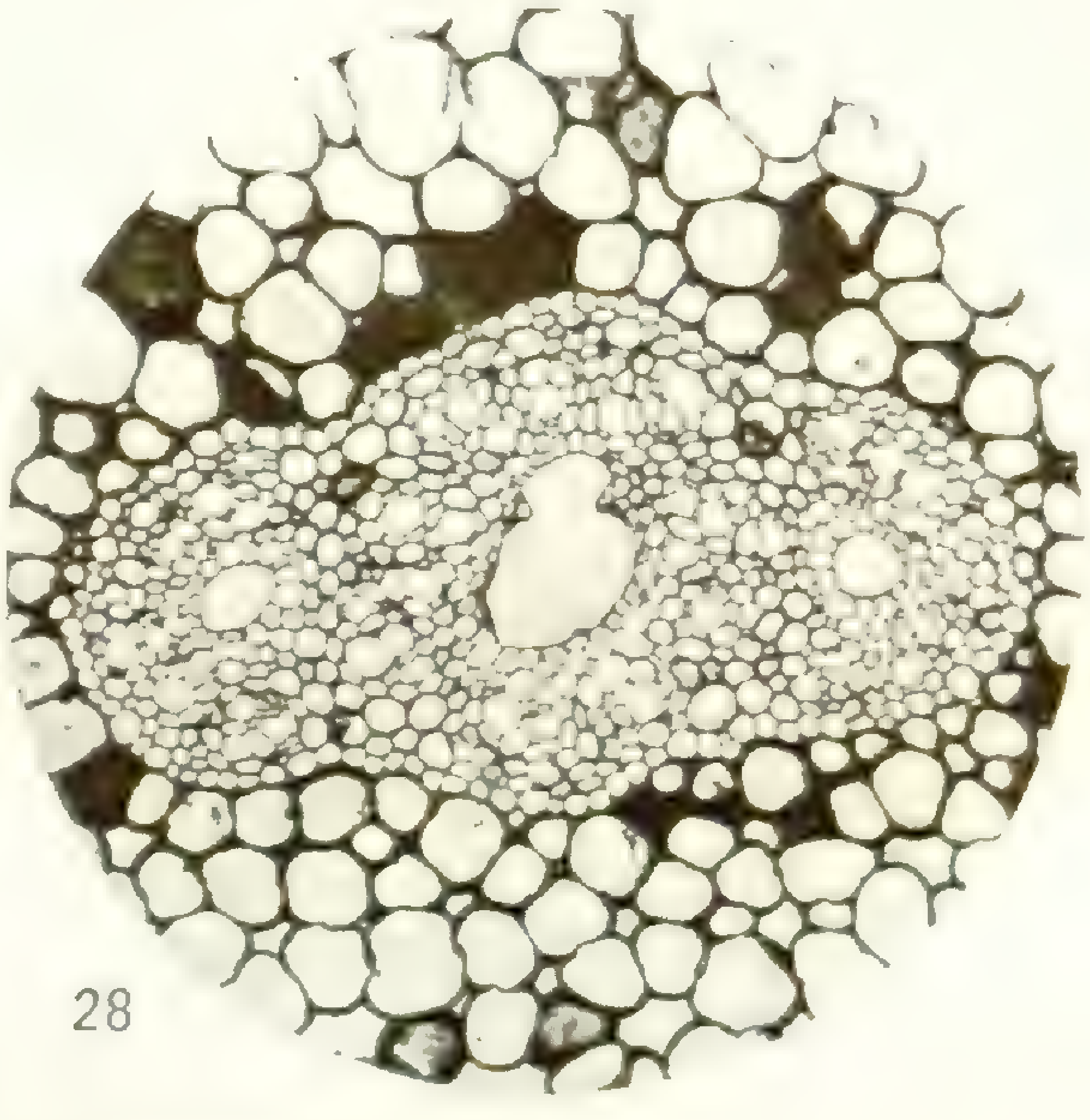

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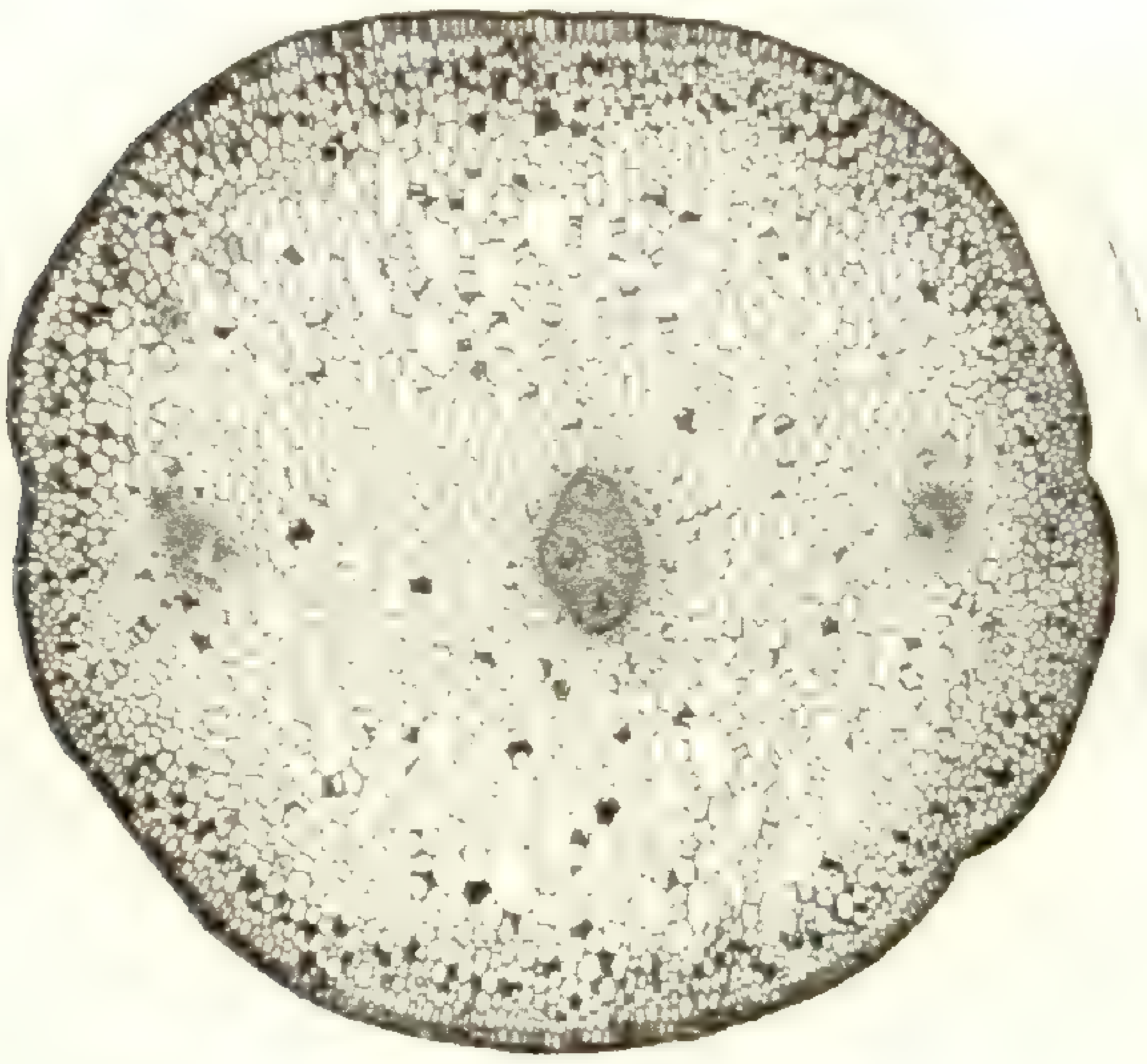
CHRYSLER on POTAMOGETONACEAE



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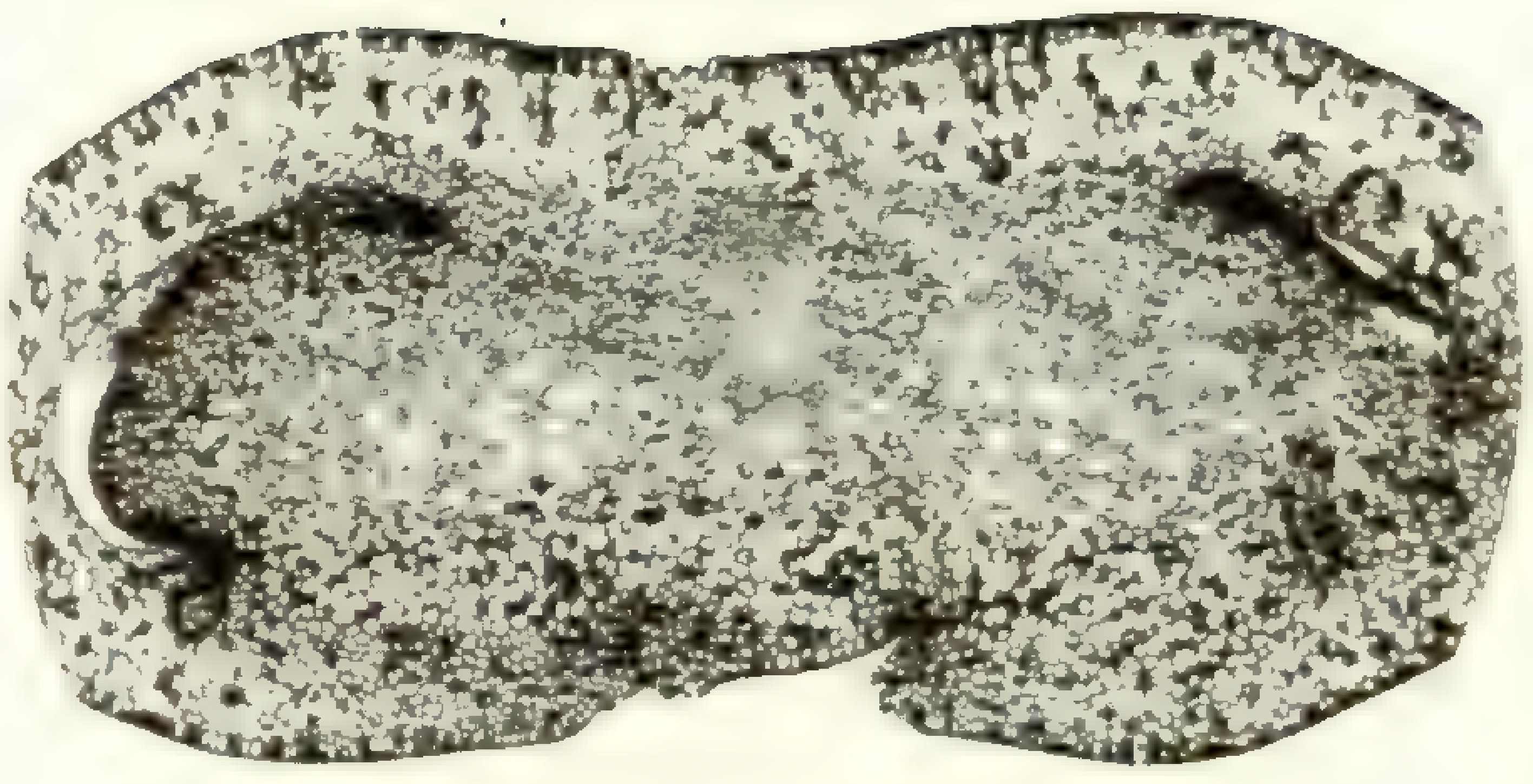

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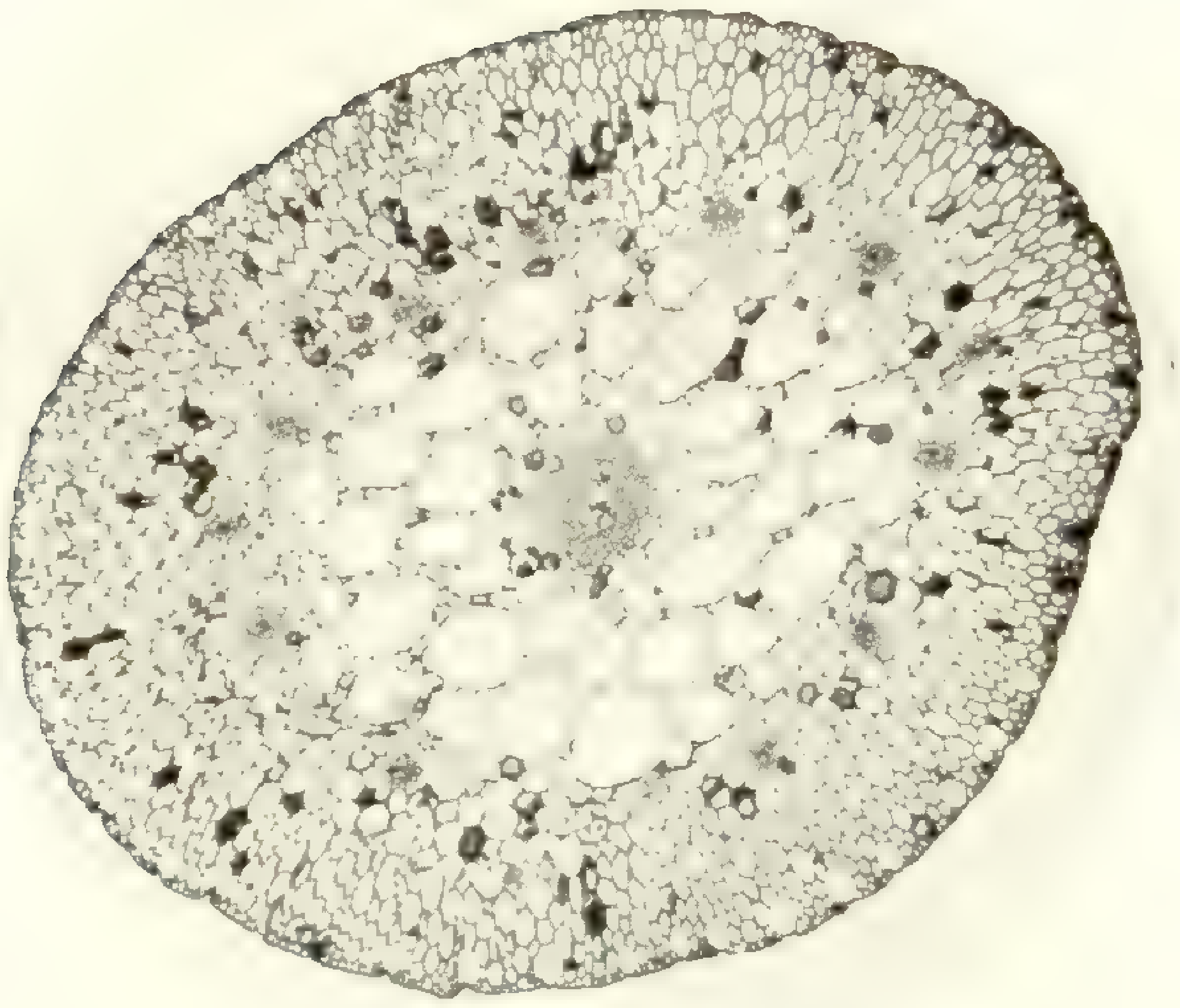

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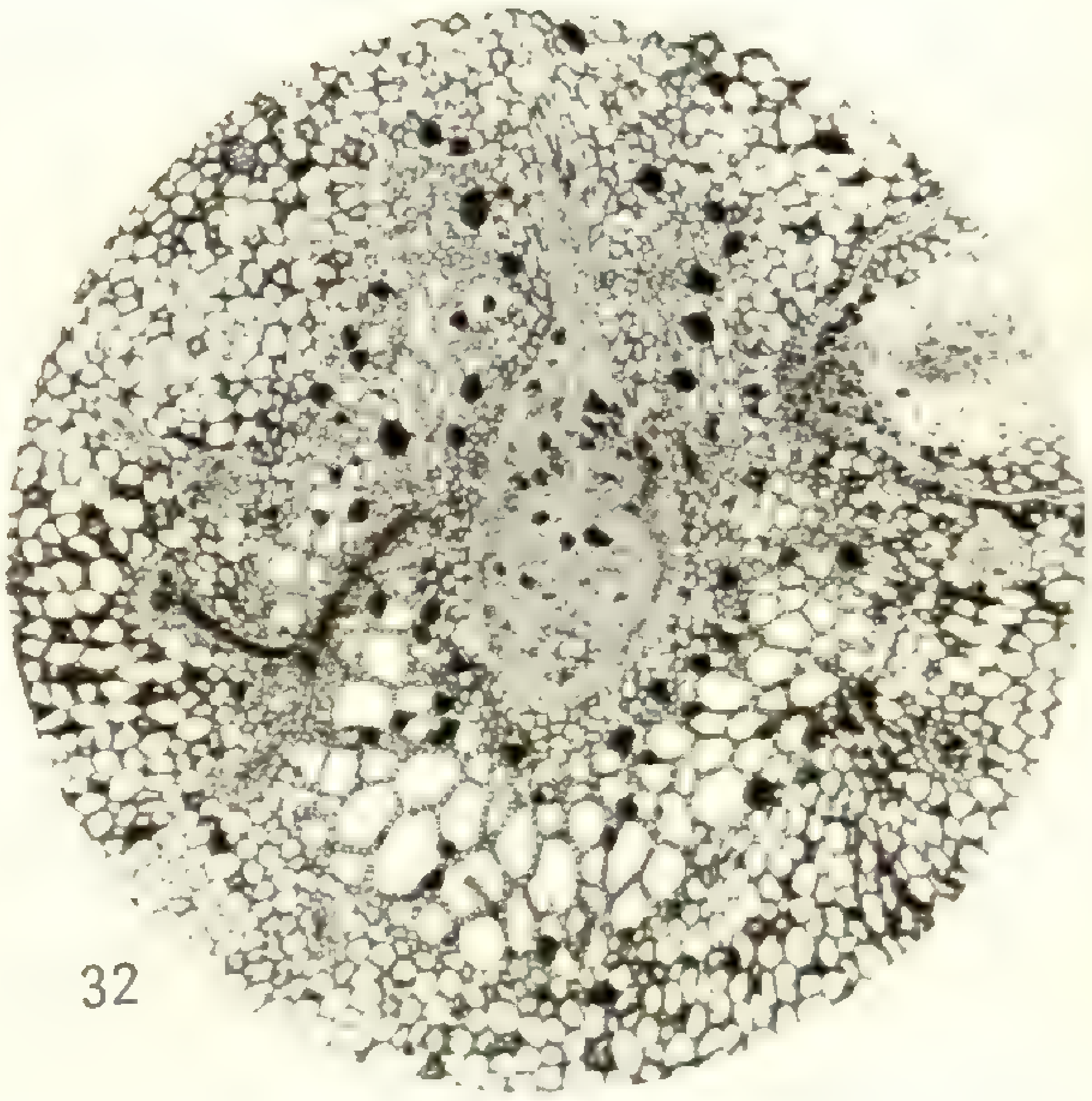

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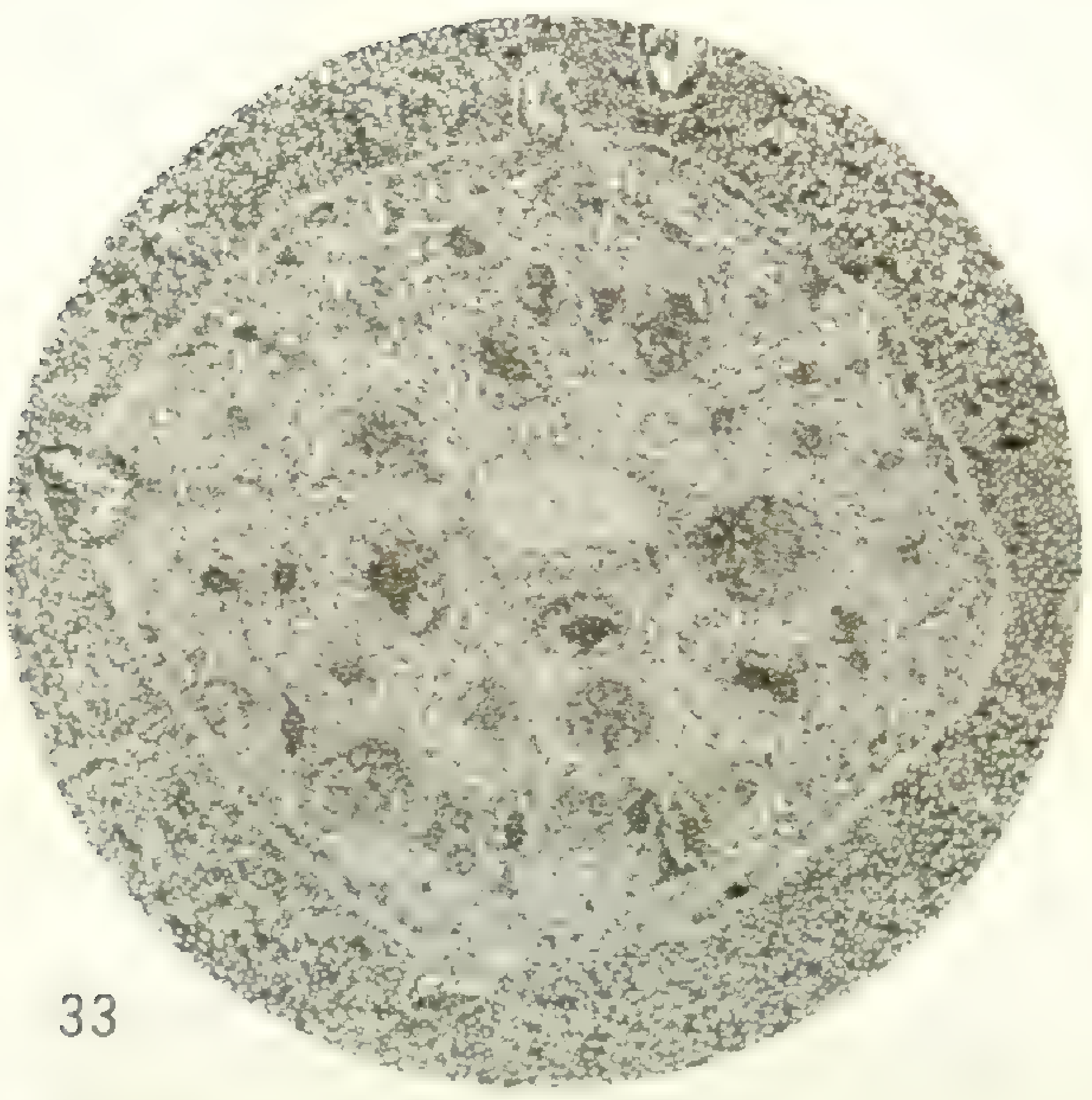

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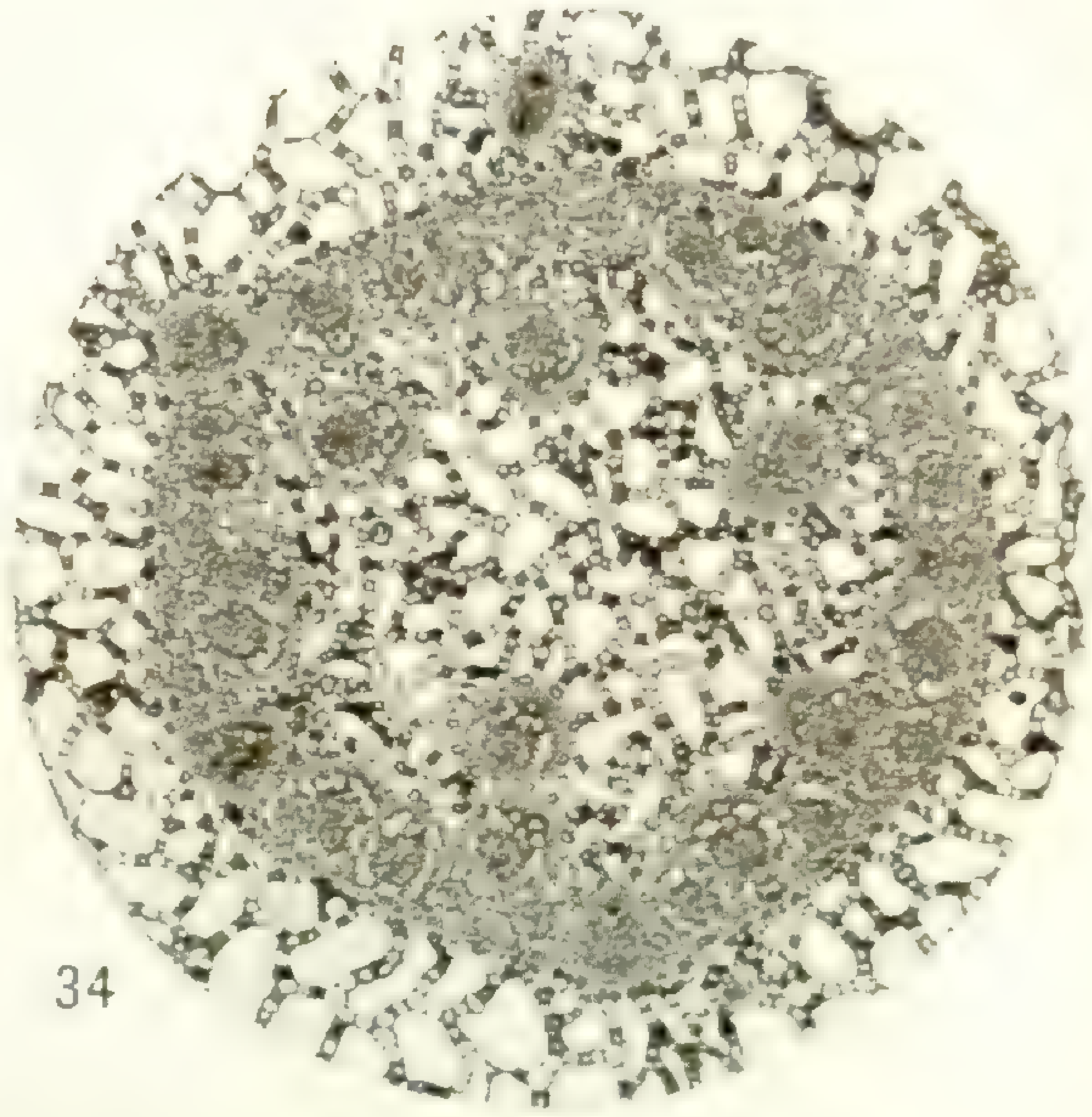

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M. A. C. photo.

CHRYSLER on POTAMOGETONACEAE

THE MALE GAMETOPHYTE OF DACRYDIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, 99

MARY S. YOUNG

(WITH PLATE XIX)

Until 1902, when COKER (**1**) published a paper on the gametophytes and embryo of Podocarpus, we had no account whatever of any of the Podocarpineae. The fact that they are in the main forms of the southern hemisphere has made it hard to secure the necessary material. COKER'S study was made from two cultivated trees, and his results, so far as the male gametophyte is concerned, were, very briefly, as follows: (1) The pollen grain contains two prothallial cells; the first degenerates slowly, the nucleus of the second slips out into the general cytoplasm and may divide; the first may segment. (2) The mature pollen grain sometimes contains as many as six nuclei. (3) There is one functional male cell formed.

In connection with these results it is interesting to note some recent work on Araucarineae. In 1905 THOMPSON (**2**) found in the pollen tubes of Agathis supernumerary nuclei, sometimes as many as thirteen, but was not certain of their origin. In the same year he found a similar condition in Araucaria, and in one instance at least, there were more than thirty nuclei placed fore and aft. In 1905 LOPRIORE (**4**) described the pollen grains of *Araucaria Bidwillii*. According to his account, two lenticular cells are successively cut off from the main body of the spore, and from them a complex is developed. The free central nucleus and an inner cell of the complex increase in size and undergo no further divisions; they remain distinct from the others, and even in the germinating tube can be recognized. One of them is figured with a conspicuous envelope of cytoplasm rich in starch. The complex increases to about fifteen cells when the walls disappear. Nuclear division, however, continues until there are about thirty-six free nuclei in the general cytoplasm. LOPRIORE interprets the cell complex as representing an antheridium and considers the two large nuclei as vegetative in character. The paper has been reviewed by

CHAMBERLAIN (5), who suggests that the complex is prothallial and the two nuclei reproductive.

In 1904 JUEL (6) found in the pollen tubes of *Cupressus Goveniana* a complex of male cells; sometimes there were only four, but more often eight or ten, and in one case about twenty. The tree was grown in a greenhouse and may not have been normal. Recently, however, a study of *Microcycas calocoma* by CALDWELL (7) has revealed a somewhat similar multiplication of reproductive cells. He found in the pollen tube a tube nucleus, a prothallial cell, a stalk cell, and eight or nine body cells. Each of these body cells later divides to form two sperm mother cells.

The peculiarity of the pollen grains of Podocarpus and its possible bearing on the question of relationships among conifers added considerable interest to the study of Dacrydium. A brief summary of some points in our present knowledge of the male gametophytes of conifers may be useful.

1. *Prothallial cells.*—Taxineae, Taxodineae, and Cupressineae have none. In Abietineae there are two and both are ephemeral. In Podocarpus there are originally two; one at least is persistent and may divide. In Araucaria, as CHAMBERLAIN interprets LOPRIORE'S figures, there is extensive prothallial tissue.

2. *Generative cells.*—The free nucleus of the spore divides to form the generative cell and tube nucleus. Usually the generative cell divides periclinally to form the so-called stalk and body cells, of which the former is sterile.

3. *The male cells.*—The body cell divides to form two male cells or nuclei. The sperms are usually unequal, but in Taxodium and Juniperus, and perhaps in Pinus, they are equal. A complex of male cells has been found in *Cupressus Goveniana.*

4. *Shedding.*—The usual shedding-stage is after the division into tube nucleus and generative cell; but in Juniperus and Cupressus the microspores are shed before any division has taken place; and in Picea the generative cell has divided.

DACRYDIUM

The material for the present work was collected by Professor L. COCKAYNE in December 1906 and January 1907 in New Zealand.

It was killed and preserved in 70 per cent. alcohol and formalin, imbedded in paraffin, cut 5 μ, and stained part in 0.5 per cent. hematoxylin and orange G and part in safranin and gentian violet. The material consisted of staminate strobili of *Dacrydium biforme, D. Bidwillii, D. cupressinum*, and *D. laxifolium*, and young ovules of *D. cupressinum, D. laxifolium*, and *D. intermedium*. Unfortunately, it was impossible to obtain a complete series from any one species. The first named was in the microspore stage only; the second furnished a series from the microspore up to the shedding of the pollen; the pollen of the third was ready to be shed, but no grains were found in the ovules; the fourth showed young tubes in the micropyles, and in *D. intermedium* they had penetrated the nucellus.

The staminate strobili are 2 to 6^{mm} in length and terminate short branches. The nucleus of the microspore is large and lies near the base of the spore, that is, the side opposite the wings (*fig. 1*). The first division cuts off a lenticular prothallial cell which lies close against the basal wall (*fig. 2*). Another division soon follows, cutting off from the main body of the spore a second prothallial cell, similar to the first and overlying it (*figs. 3, 4*). Both these cells have distinct though very delicate walls; their nuclei are somewhat flattened and stain very deeply, but they show no sign of degeneration; the cytoplasm also is very dense.

In Dacrydium, as in Podocarpus and the Abietineae, a third cell is now cut off from the main body of the spore (*fig. 5*). It overlies the others and is so similar to them that but for its subsequent behavior one might think it a third prothallial cell. It is a generative cell—generative in the sense that it is the ancestor of sperms. This and the second prothallial cell now both divide; usually the division of the latter occurs first, but the order may be reversed (*figs. 6, 7*). In either case the result is a complex of five distinct cells, one in the lowest, and two in each of the upper tiers, filling about one-third of the cavity of the spore. All the five nuclei are oval and stain very deeply. The free nucleus, which is now the tube nucleus, divides no more. It is somewhat irregular in outline and is larger and less dense than any of the others. The cytoplasm of the pollen grains is at this time considerably vacuolated.

Up to this point all the stages described were obtained from *D.*

Bidwillii. A very close series was secured, showing spindles in every one of the divisions, so that the sequence of events was quite clear. In this species, very rarely, a division of the first prothallial cell occurs. In *D. cupressinum,* however, this takes place normally, giving a complex of six instead of five cells (*fig. 11*). As early stages were not secured, I cannot say when the division occurs.

The next step in the development of the gametophyte is the enlargement of the two generative daughter cells. They increase in thickness and the nuclei lose their flattened appearance. Before this there had been nothing by which to distinguish between the two, but now one of them grows more rapidly than the other and arches upward conspicuously. This may take place before or after the division of the second prothallial cell. At the same time the upper and inner walls become gradually less and less distinct and finally disappear altogether (*figs. 8, 9, 10*). The larger cell does not lose its identity, but retains about itself a sheath of cytoplasm, rich in starch. It abandons all connection with the spore wall and appears as a rounded cell free within the pollen grain, similar to the body cell of other conifers. The other loses itself in the general cytoplasm and its nucleus is set free.

The prothallial cells now also increase somewhat in thickness, their nuclei round up, and their walls fade away. When ready to be shed, the pollen grain of *D. Bidwillii* contains the body cell and five free nuclei. These change their relative positions somewhat, and the nucleus of the body cell is indistinguishable from those of the prothallial cells and the tube nucleus.

Several pollen grains of *D. Bidwillii* were found in which two body cells were apparently developing from the divided generative cell; though these were unequal in size, both had the characteristic sheath. In two or three older pollen grains of *D. laxifolium,* in which the tubes were formed, there was the appearance of two body cells, one larger than the other; *fig. 13* shows one of these cases, though not the most pronounced.

D. laxifolium, though collected on the same day with the microspores of *D. biforme* and the more advanced *D. Bidwillii,* showed no young stages at all. The pollen had all been shed. The micropyles were full of the pollen grains, of which some had not germinated, but some had tubes twice the length of the spore. In these there appeared always the conspicuous body cell and six free nuclei. Among the latter one could sometimes recognize the tube and generative daughter nuclei by their position or appearance, but sometimes they were quite indistinguishable. In several cases one, presumably the tube nucleus, had entered the tube and the others were about to follow it (*figs. 12, 13*).

From the number of free nuclei, it is fair to infer that in *D. laxifolium*, as in *D. cupressinum*, the first prothallial cell has divided. Another possible explanation would be the division of the body cell, but the latest stages in *D. Bidwillii*, in which the shedding of the pollen had begun, could not have been much earlier than that of the ungerminated pollen grains in the micropyles, and there was no evidence of such a division in either of these. In several cases, too, the position of two free nuclei side by side against the lower wall suggested their origin from the first prothallial cell.

The latest stages found were in *D. intermedium* collected January 31. The tubes had penetrated the nucellus to some distance, and free nuclei were seen in them, but there was no evidence of any further divisions. The body cell, still undivided, remained alone in the cavity of the pollen grain. It seemed probable that it would have divided and given rise directly to two sperms, as in other conifers, but there might be other divisions previous to sperm formation. It is hoped that in the near future material can be secured and the life-history completed.

DISCUSSION

The striking facts about the male gametophyte are (1) the multiplication of prothallial cells and (2) the transverse division of the generative cell. The development in Dacrydium agrees rather closely with that described by COKER for Podocarpus, except that there is no sign of degeneration of any of the cells, and the division of the generative cell in Podocarpus was not observed. In the light of what we now know about Podocarpineae, one can hardly study LOPRIORE's drawings of Araucaria without agreeing with CHAMBERLAIN's view. The mode of origin of the cell complex at once suggests the prothallial cells of other conifers, and the large nucleus with its cytoplasmic sheath looks too much like a body cell to be called vegetative. In fact, all the early figures up to the five-cell stage might be taken to represent *Dacrydium cupressinum*. These show the formation of first and second prothallial cells, the generative cell, and the division of the first prothallial cell. According to LOPRIORE'S account, however, after the first two divisions it is usually the middle, that is the second prothallial cell, which divides longitudinally, cutting off what we would call the generative cell.

The complex in Cupressus is not at all comparable to that of Araucaria, for it has a wholly different origin. It is not formed early in the history of the gametophyte by successive divisions of the spore, but later, in the tube, by the division of a single differentiated reproductive or body cell. The rarity of any prothallial cells at all in conifers sets apart Abietineae, Podocarpineae, and Araucarineae as the possible representatives of a more primitive condition. Araucaria seems to point toward an ancestral functioning thallus, and Dacrydium shows a further step in the reduction so nearly accomplished in Pinus. A possible connection between the three groups is suggested. The question of relationships, however, can be answered only through the combined results of various lines of research.

In most conifers that have been studied, the generative cell divides periclinally to form the so-called stalk and body cells, but outside of conifers we find Cycas and Ginkgo in which the division is transverse. The term "stalk cell" is a rather unfortunate one. Its use was suggested by the position of the cell between the body and the prothallial cells, but in the case of a transverse division, or where, as in Sequoia and Cryptomeria, the division takes place in the free condition in the tube, the significance of the name is entirely lost. It is perhaps misleading, too, in the suggestion of the stalk of an antheridium.

The generative cell is the first of a spermatogenous series. In Pinus, for example, it divides, giving rise to a sterile and a fertile cell. The body cell divides once and produces two male cells. In Dacrydium also the first division gives rise to a fertile and a sterile cell, but with a tendency for both to function. In Microcycas the generative cell produces the sterile stalk cell and eight or more body cells. In *Cupressus Goveniana* one at least of the two generative daughter cells divides many times, giving rise to extensive fertile tissue. JUEL saw a small nucleus which he thought to be the stalk nucleus. From Microcycas, then, through Dacrydium to Pinus we have a reduction series in the spermatogenous tissue. The inequality of the sperms, so common in conifers, is only a further step in this reduction.

The tendency for two body cells to develop in Dacrydium may be related to the transverse division of the generative cell. In Pinus the inner cell has the advantage at the start, and is thus set apart as the body cell; but in Dacrydium both cells begin exsistence with apparently even chances, being equally free to enlarge. Thus it seems at first a matter of indifference which shall be the body cell and which sterile, and some accident of slightly superior size or better nourishment may be the determining factor.

SUMMARY

1. There are two prothallial cells cut off from the main body of the spore. In *Dacrydium Bidwillii* usually only the second divides; in *D. laxifolium* and *D. cupressinum* both divide.
2. The generative cell divides by an anticlinal wall, one daughter cell functioning as a body cell and the other being sterile. In some cases both produce body cells.
3. The walls of the prothallial cells and the two generative daughter cells disappear.
4. The mature pollen grain contains the body cell and five or six free nuclei, according as the first prothallial cell has or has not divided.

This work was carried on under the direction of Professor J. M. COULTER and DR. C. J. CHAMBERLAIN.

UNIVERSITY OF CHICAGO

NOTE.—Since this investigation was completed, a paper by JEFFREY and CHRYSLER (The microgametophyte of the Podocarpineae. Amer. Nat. **41**: 355–364. 1907) on the same subject has appeared. The paper deals chiefly with Podocarpus. The development of the gametophyte corresponds in general with that of Dacrydium, but with further divisions of the prothallial cells, resulting sometimes in eight, and an occasional division of the generative cell into three instead of only two cells.

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EXPLANATION OF PLATE XIX

A Zeiss apochromatic 2^{mm} homogeneous immersion objective and compensating ocular 8 were used. All drawings were made with a camera lucida and reduced one-half, giving a magnification when reduced of 960 diameters.

Abbreviations: *t*, tube nucleus; *g*, generative cell; p_1, first prothallial cell; p_2, second prothallial cell; *b*, body cell; *s*, spermatogenous cell; *st*, starch.

Figs. 1–10, Dacrydium Bidwillii

FIG. 1. Microspore.

FIG. 2. First prothallial cell cut off.

FIGS. 3, 4. Cutting-off of second prothallial cell.

FIG. 5. Cutting-off of generative cell.

FIG. 6. The second prothallial cell divided.

FIG. 7. Division of generative cell.

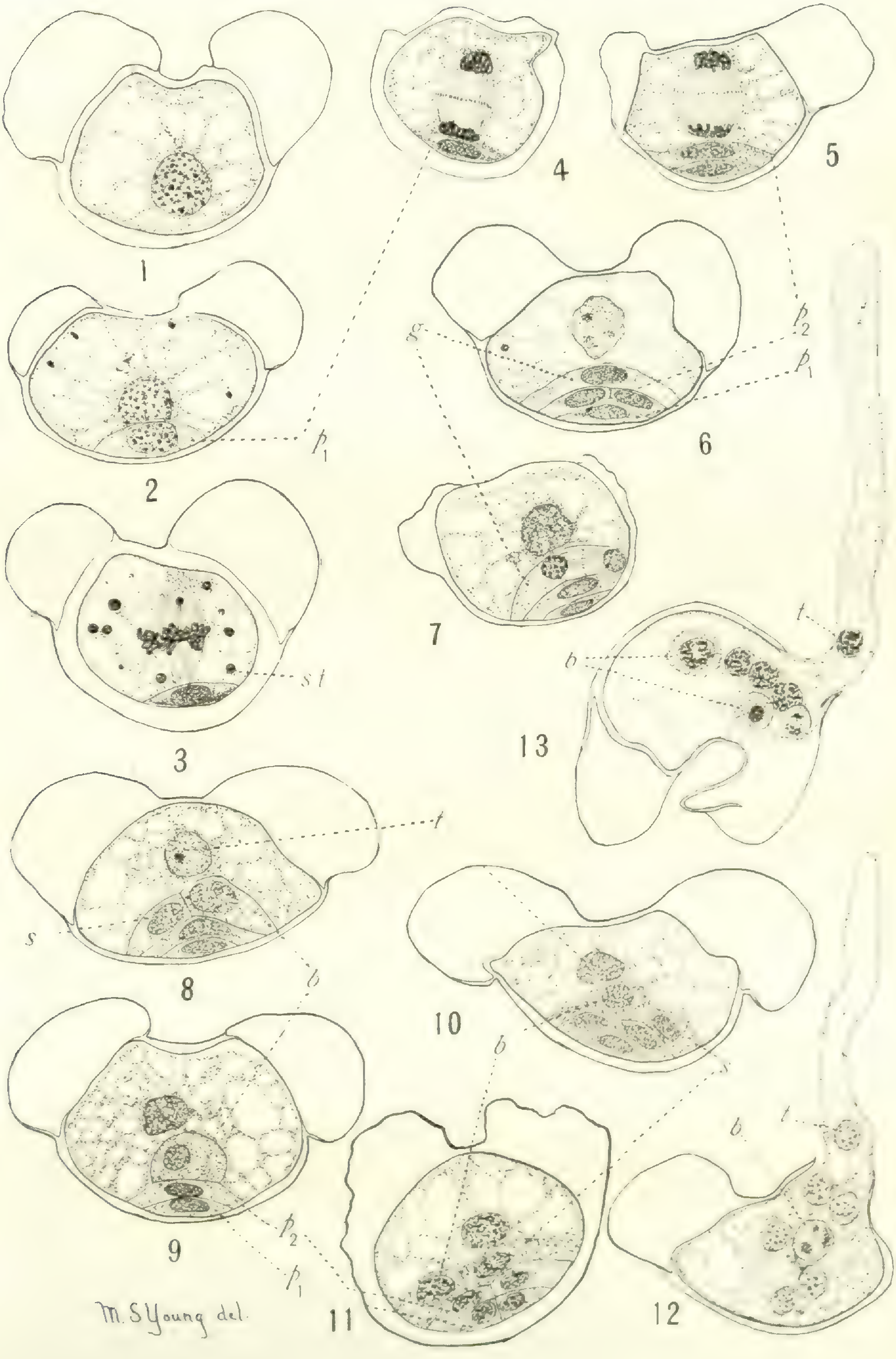
FIG. 8. The generative cell divided, the two daughter cells enlarging.

FIG. 9. Tube nucleus, body cell, and two prothallial cells; stalk cell not shown.

FIG. 10. Walls of stalk and body cells disappearing.

FIG. 11. *Dacrydium cupressinum;* both prothallial cells divided.

FIGS. 12, 13. *Dacrydium laxifolium;* tube nucleus entering the tube; body cell and prothallial and stalk nuclei in the grain.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YOUNG on DACRYDIUM

BRYOLOGICAL PAPERS

I. THE ORIGIN OF AIR CHAMBERS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, 100

CHARLES R. BARNES and W. J. G. LAND

(WITH TWENTY-TWO FIGURES)

The air passages in certain tissues of the vascular plants are so prominent as to attract instant attention when a section is examined. Inasmuch as new cells are produced by division, and the partitioning wall is a joint product of the two severed protoplasts, a-priori reasoning leads to the hypothesis that intercellular spaces arise by the secondary splitting of the membrane, on account of unequal growth and turgor. This hypothesis is abundantly verified by observation, and there remains no doubt whatever that the aerating passages of vascular plants are formed in this manner.

When intercellular spaces were observed in liverworts, it was natural to assume that they took their origin in the same fashion. In the Anthocerotales, intercellular spaces of the triangular and quadrangular type, familiar in the pith parenchyma of vascular plants, occur in both gametophyte and sporophyte. We are not aware that the origin of these has ever been supposed to be in any way different from that of similar spaces elsewhere. The origin of the mucilage clefts and chambers of Anthoceros and Dendroceros is definitely ascribed by LEITGEB[1] to cleavage, and he has been quoted in all textbooks.

In the Marchantiales, however, the canals and air chambers in the upper portion of the thallus are so large and extraordinary in architecture, that it was questionable whether they arose in the familiar fashion, or had some peculiar origin. HOFMEISTER[2] describes the formation of the air chambers in the gametophore of *Marchantia polymorpha* in these words:

> Close under the arched upper surface of the receptacle of Marchantia . . . . numerous air cavities are formed, even before the first appearance of the arche-

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[1] LEITGEB, H., Untersuchungen über die Lebermoose 5:4, 13ff., 31. 1879.

[2] Higher Cryptogamia 117. 1862.

gonia. They are formed in the same manner as the air cavities of the stem. At the first appearance of the air cavity one epidermal cell only detaches itself from the underlying tissue of the receptacle. By repeated transverse division of the mural rows of cells lying between the air cavities, the lid of the cavity is carried rapidly upwards. This epidermal cell, which closes the air cavity, forms itself into a stomate.

HOFMEISTER also speaks of air cavities being formed in the "stem" by the lifting-up of a "single layer of cells," of which the central one divides to form the ring that opens as a stoma.

This conception is obviously that of schizogenous formation, but the separation was ascribed to the upgrowth of the lateral walls of the chamber as the base and roof widen. With the exception of the detachment of a single epidermal cell, what HOFMEISTER describes actually happens; but he observed only the later stages of development and not the origin of the chambers.

This alleged origin was accepted by SACHS and was described by him in the *Lehrbuch der Botanik* of 1874, whence it found its way into the English edition, issued in 1882. There the statement occurs (under the topic *Intercellular spaces*, be it noted):

> The epidermal cells become detached from those lying beneath over rhomboidal areas, which are marked off from one another by walls formed of cells which are not detached.

In the Appendix (p. 948), VINES, who had seen LEITGEB'S paper on the stomata of Marchantia,[3] gives a very brief and clear outline of the formation of air chambers according to LEITGEB. From that time to the present LEITGEB'S views have prevailed, being repeated in all the textbooks as settled fact. As CAMPBELL in the new edition of *Mosses and ferns* nowhere definitely describes the origin of air chambers,[4] we quote and translate from GOEBEL'S *Organographie* (p. 296):

> It is characteristic of the Marchantiaceae and Ricciaceae that air chambers are found in the nutritive tissues. These arise, as LEITGEB first showed, not at

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[3] Sitzb. Kais. Akad. Wiss. Wien **81**:40–54. *pl. 1.* 1880.

[4] CAMPBELL casually uses this expression (*op. cit.*, p. 39) regarding *Riccia trichocarpa:* "At first the cells of the young thallus are without *intercellular spaces*, but at an early period the outer cells of the young segments *separate* and form the beginnings of the characteristic air-spaces" [italics ours]. Inasmuch as CAMPBELL follows LEITGEB'S account for other Ricciaceae, so far as he gives any description of the air-chamber formation, these phrases seem to have been accidentally correct.

all as do the intercellular spaces of higher plants, by the cells separating, nor even by progressive cleavage from outside inward; but they appear originally as depressions in the surface, which arise by definite points (always situate where four cells meet) lagging in growth and so becoming overgrown by the adjacent parts.

While casually following the development of the spirelike air chambers on the gametophore of a species of Fimbriaria collected by Dr. C. J. CHAMBERLAIN in Mexico in 1904,[5] our attention was attracted to very young air chambers on a receptacle still very small. The appearance of a cavity very close to the apical cell, and relatively deep in the tissue, raised a doubt as to the possibility of its having been overgrown so promptly by adjacent cells. On examining this matter in the thallus, in longitudinal sections through the apical cell, what we saw showed that a reinvestigation of the origin of the air chambers was needed.

Accordingly, we have examined as many of the Marchantiales as have been easily obtainable. Although we have not studied all the members of the group, but only representatives, the facts observed are so uniform and unambiguous that it is unlikely there is any other mode of origin than the one found in every case examined. This expectation derives force from the fact that our examination has covered all types of air chamber, and that LEITGEB'S extensive observations can be interpreted (as he himself confessed in regard to Marchantia and Preissia) in consonance with schizogenous origin.

Inasmuch as LEITGEB'S view is accepted at present and we consider it untenable, we quote some of his very unequivocal declarations, to show that he has left no doubt as to his meaning. Speaking of the Ricciaceae, after describing the quadratic surface mesh formed by the walls of the cells near the growing point, he says:[6]

> Soon one observes at the corners small pits, which arise thus: the growth of the lateral walls of the outer cells, in so far as concerns the direction at right angles

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[5] Probably *Fimbriaria echinella* Gottsche.

[6] Bald bemerkt man an den Ecken kleine Grübchen welche dadurch entstehen, dass das Wachsthum der Seitenwände der Aussenzellen, insoweit als es sich in der auf der Dorsalfläche senkrechten Richtung vollzieht, in den Kanten geringer ist, als an den übrigen Stellen. Es entspricht daher der tiefste Punkt eines Grübchens dem (ursprünglich an der Oberfläche gelegenen) äussersten Punkte der verkürzt bleibenden Seitenkante, und die das Grübchen umgrenzenden Wandstücke sind Theile der ursprünglichen Aussenwände, resp. aus diesen hervorgegangen. Indem nun dieser

> to the dorsal surface, is less at the corners than in the other parts. The lowest part of a pit therefore corresponds to the outermost point of the lateral wall, originally lying in the surface, which wall remains short, and the parts of the wall bounding the pit are parts of the originally outer walls, or have arisen from them. If this mode of growth be continued, the pit will of course be deepened. Now there occurs in each cell a division parallel to the surface, which separates approximately the part surrounding the pit from the inner part. From the exterior cell thus formed, there arises the whole of the tissue pervaded by air chambers. First of all, the pit becomes farther deepened into a canal by progressive growth in the same direction, and now there follows, in each outer cell, a division parallel to the earlier one. The canal now penetrates two layers of cells, of which the outer becomes the permanent epidermis, while from the inner arises the entire tissue containing the air chambers lying beneath the epidermis.

He continues:[7]

> By way of summary of the foregoing exposition of the formation of air chambers and stomata, it may be said that *the air chambers do not arise in the tissue by the separation of cells, nor by a progressive splitting from outside inward;* but that they represent depressions of the surface, which are formed by definite points of the surface becoming overgrown by the more rapid growth of neighboring parts.

This investigation LEITGEB extended by a study of the stomata of Marchantiaceae, an account of which, published in 1880 (*l. c.*, footnote 3), was reprinted, with only a few unimportant verbal changes, in the last part of the *Untersuchungen*. After declaring the homology of the air chambers and canals of Marchantiaceae with those of

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Wachsthumvorgang noch weiter eingehalten wird, wird das Grübchen selbstverständlich vertieft. Nun erfolgt in jeder Zelle eine der Oberfläche parallele Theilung, welche ungefähr den die Grube umgrenzenden Theil derselben von dem inneren Theile abschneidet. Aus den so entstandenen Aussenzellen geht nun das ganze, mit Lufträumen durchzogene Gewebe hervor. Vorerst wird durch das in gleicher Richtung fortschreitende Wachsthum das Grübchen weiter vertieft und so zum Canale, und nun erfolgt in jeder Aussenzelle eine der früheren parallele Theilung. Der Canal durchsetzt nun zwei Zelllagen, deren äussere zur bleibenden Oberhaut wird, während aus der inneren Zellschicht die ganze unter der Oberhaut liegende Lufthöhlenschichte hervorgeht.—Untersuchungen über die Lebermoose 4:10. 1879.

[7] In Zusammenfassung der über die Bildung der Lufträume und Spaltöffnungen eben gegebenen Ausführungen ergibt sich also, dass die Luftkammern nicht *im* Gewebe durch Auseinanderweichen der Zellen entstehen, auch nicht durch eine von aussen nach innen fortschreitende Spaltung; sondern dass sie Einsenkungen der Oberfläche darstellen, die dadurch gebildet werden, dass bestimmte Punkte der Oberfläche durch rascheres Wachsthum benachbarter Partieen überwachsen werden.—*l. c.*, p. 12.

Ricciaceae, and pointing out the existence of intermediate forms, he says:[8]

> Further, there does not occur in the formation of the air chamber any separation of cells previously joined without interstices; nor does the roof of the air chamber (epidermis) lift itself up secondarily from the underlying tissues, but it is formed simultaneously with the rudiment of the air chamber and grows in breadth at equal pace with the broadening chamber.

Regarding Preissia he repeats:[9]

> It (the formation of air chambers) begins with the formation of superficial pits, which deepen to canals that later become closed again outwardly, as in the carpophore.

And further:[10]

> I have not discussed hitherto the origin of these primary pits. We *might* explain them by the splitting of the membrane, i. e., the separation of cells; and the formation of aerating apparatus with simple openings would then be con-

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[8] Es findet also bei Bildung der Luftkammer eine Trennung früher interstitienlos verbundener Zellen nicht statt, und die den Luftraum nach aussen abschliessende Decke (Oberhaut) hebt sich nicht secundär vom darunter liegenden Gewebe ab, sondern sie bildet sich schon zugleich mit der Anlage des Luftraumes, und wächst nach Massgabe seiner Verbreiterung ebenfalls in die Breite.—Unters. über die Lebermoose 6:6. 1881.

[9] Sie beginnt mit der Bildung von oberflächlichen Grübchen, die sich zu einem Canale vertiefen, der später wie an den Fruchtköpfen nach aussen wieder verschlossen wird.—*l. c.*, p. 9.

[10] Ich habe bis jetzt der Art der Entstehung jener primären Grübchen nicht Erwähnung gethan. Wir könnten sie durch Spaltung der Membran, d. h. durch Trennung der Zellen erklären, und es würde dann die Bildung des mit einfachen Oeffnungen versehenen Athmungsapparates als Folge einer von aussen nach innen fortschreitenden Membranspaltung zu betrachten sein, wo also die Bildung der Oeffnung der primäre, die der Athemhöhle (Luftkammer) der secundäre Vorgang wäre. Am Laube von *Marchantia* (und *Preissia*) würde aber zuerst die Athemhöhle, und zwar wieder durch Trennung der Zellen (Membranspaltung) erfolgen, und später erst würde der Athmungscanal—und wie die Beobachtung lehrt—von innen nach aussen fortschreitend gebildet werden. Für die Oeffnungen an den Fruchtköpfen müsste man selbstverständlich annehmen, dass hier ebenfalls die Spaltung von aussen nach innen fortschreite, dass die Spalte aber später durch Aneinanderschliessen der Zellen wieder verschwinde, um erst weit später wieder geöffnet zu werden.

Ich glaube aber, dass eine andere Erklärung viel plausibler ist, weil sie geeignet ist, die Vorgänge von einem Gesichtspunkte aus zu betrachten, und sie mit anderen scheinbar ganz verschiedenen Bildungen in Uebereinstimmung zu bringen.

Ich habe im IV. Hefte meiner Lebermoosuntersuchungen die Ansicht aufgestellt, und zu begründen versucht, dass jene primären Grübchen nicht durch Membranspalsidered as a result of progressive cleavage of the membranes from outside inward, when the formation of the opening would be the primary, and that of the air chamber the secondary process. So on the frond of Marchantia (and Preissia) the air chamber would arise first (and indeed by cleavage of the cell walls), and only later would the aerating canal be formed (as in fact observation shows) progressively from inside outward. As to the openings on the carpophore, one of course would have to assume that here likewise the cleavage advances from outside inward, but that the cleft later disappears, on account of the pressing together of the cells, and only much later again becomes opened.

But I think that another explanation is much more plausible, because it is competent to consider the processes from a standpoint which brings them into harmony with other entirely different structures.

In part IV of my *Untersuchungen* I have set forth and sought to establish the view that each primary pit is not formed by cleavage of membranes,but arises in consequence of peripheral growth in thickness. The deepest point of the pit thus does not correspond with a point lying originally *within* the membrane of a lateral wall, i. e., below the surface, but lay originally in the outer surface, and the parts of the wall bounding the pit are therefore parts of the original outer walls, or have developed from them. If the same growth process (which is really only accelerated growth in area of the originally free outer walls) proceeds still further, the pit will be deepened. Now as the air chambers (to be) arise exclusively by growth in area of the parts of the walls bounding the pits, it follows that they must be regarded as really depressions of the surface, which are formed by certain

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tung sich bilden, sondern in Folge des peripherischen Dickenwachsthums entstehen. Der tiefste Punkt des Grübchens entspricht somit nicht einem ursprünglich innerhalb der Membran einer Seitenwand, also innerhalb der Oberfläche gelegenen Punkt, sondern war ursprünglich, in der Aussenfläche gelegen und die das Grübchen umgebenden Wandstücke sind daher Theile der ursprünglichen Aussenwände, respective aus ihnen hervorgegangen. Indem der gleiche Wachsthumsvorgang (der eigentlich ja nur ein gesteigertes Flächenwachsthum der ursprünglichen freien Aussenwände ist) noch weiter eingehalten wird, wird das Grübchen vertieft. Da nun die späteren Luftkammern ausschliesslich durch Flächenwachsthum der die Grübchen begrenzenden Wandstücke entstehen, so folgt daraus, dass sie eigentlich als Einsenkungen der Oberfläche zu betrachten sind, die dadurch gebildet werden, dass bestimmte Punkte der Oberfläche durch rascheres Wachsthum benachbarter Partien überwachsen werden. Es trifft hier bestimmte Punkte der Oberfläche ganz dasselbe Schicksal, wie die anfangs sogar über die Oberfläche hervorragenden Mutterzellen der Geschlechtsorgane, welche ja ebenfalls durch Ueberwachsen ins Gewebe versenkt werden. Die Höhlungen, in welchen die Antheridien und Archegonien z. B. bei *Riccia* liegen, entsprechen in ihrer Bildung vollkommen den Luftkammern, und da beide gleichzeitig angelegt werden, müssen sie auch in gleiche Tiefe in das Gewebe hineinreichen, mit andern Worten, die Basis der Geschlechtsorgane liegt in gleichem Tiefe mit der innern Begrenzung der Lufträume, und wo die Organe zu Ständen zusammentreten, sind diese ihrer ganzen Tiefe nach von Luftkammern durchzogen und sitzen unmittelbar dem interstitienlosen Gewebe auf.—*l. c.*, p. 9.

> points of the surface becoming overgrown by reason of the more rapid growth of neighboring parts. There befalls these points quite the same fate as overtakes the mother cells of the sex-organs, which at first indeed project above the surface, but likewise become sunk in the tissue by being overgrown. The hollows in which lie the antheridia and archegonia (e. g., of Riccia) correspond completely in their formation with the air chambers; and as both are laid down simultaneously, they must attain an equal depth in the tissues; in other words the base of the sex-organs lies at the same level as the inner boundary of the air chambers; and where the sex-organs are aggregated in groups, they are surrounded for their whole length by air chambers and are seated directly upon the compact tissue.

There is no doubt as to LEITGEB'S meaning, for he has both put his declaration positively and denied categorically the other possible modes of origin. Yet it is clear, both from his figures and from his description, that he saw many clefts which can be most easily interpreted as due to splitting; but apparently he did not in all cases see the earliest stages of the air chambers, which can be interpreted in no other way. It is not surprising, however, that so good an observer missed them, as he had at his command almost none of the modern technique. Rather it is surprising that he saw so much and so accurately, for with the best technique it is not easy to discern the first cleavage.

A-priori reasoning, weak as it is, creates suspicion of the correctness of LEITGEB'S view, and no figure of his shows any condition that cannot be interpreted in consonance with schizogenous origin. It is peculiarly difficult to conceive of a mode of growth such as he describes, for nothing like it is known elsewhere. If the lowest point of the pit is a point which originally lay in the surface, and there is no cleavage, then the progressive formation of the pit must be somewhat as in *fig. 1*. In such a process the pit must be very slender, as otherwise the wall would show a reentrant angle; indeed, it is difficult to see why the pit would not be closed by turgor as fast as the adjacent cells grew up, unless one predicates rigidity at the base of the dome or a rapid growth at the very surface in which the upgrowing cells did not share. When ready for the divisions which are to pro-

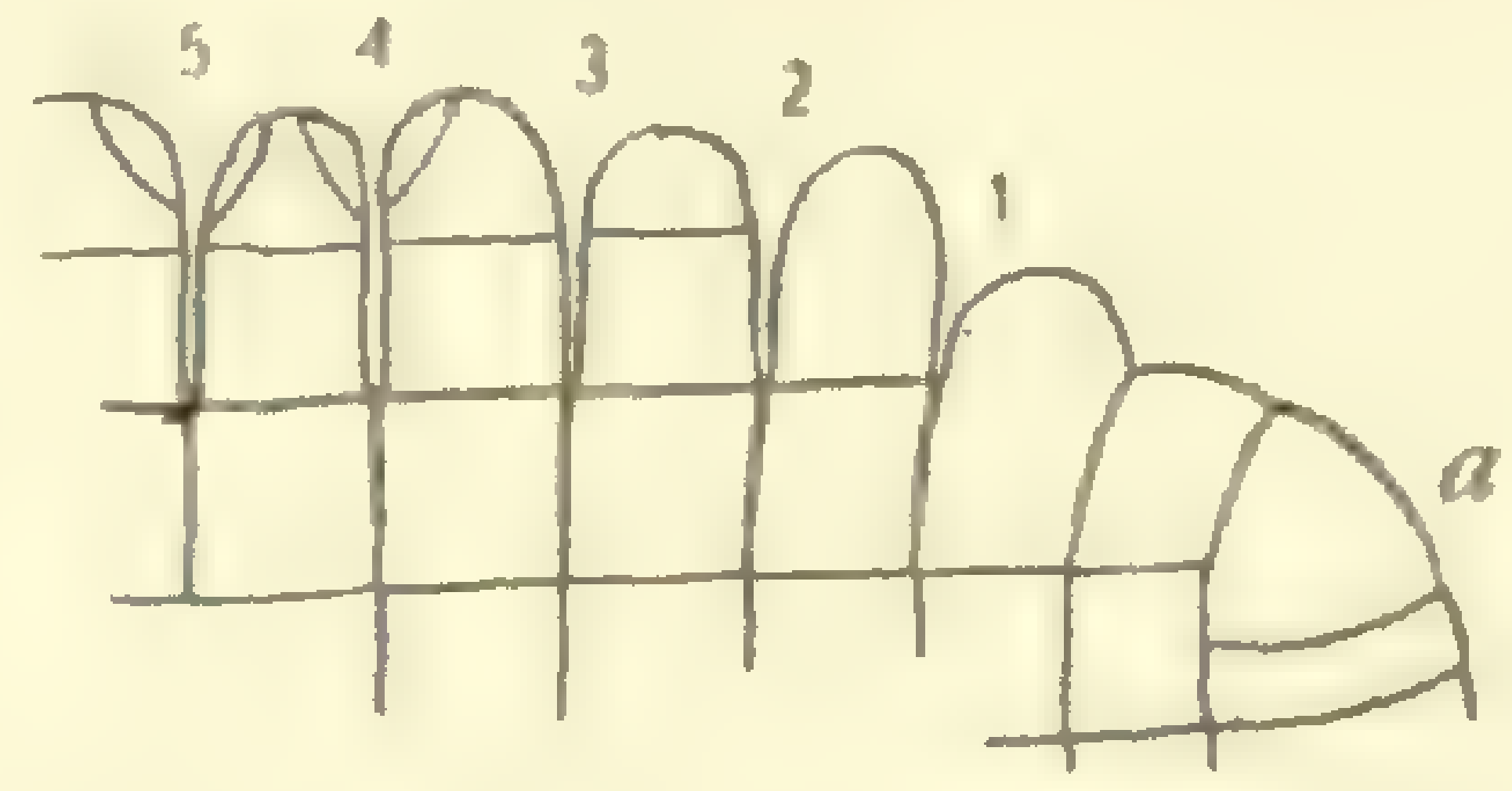

FIG. 1.—Diagram of the origin of air chambers according to LEITGEB.

vide a roof for the widening chamber, the form of the cell, necessary under this mode of growth, would seem almost to preclude so unequal a division (4, *fig. 1*). Certainly if the pit were open at the time the first division took place, the cells cut off could only close it by later growth. As a matter of fact, in LEITGEB'S plates no such stages as we have sketched are shown; yet if the pit is formed as he says, they should be found. In spite of diligent search we have seen nothing that could possibly be interpreted so.

Moreover, it is easy to see that LEITGEB was misled by his desire to homologize the formation of air chambers with the formation of pits for the sex-organs. So, though he admits seeing the primary formation of intercellular spaces in Marchantia, Preissia, and Plagiochasma, he deliberately rejects the obvious explanation of splitting. He did this in order to apply to Marchantiaceae the idea he had conceived for Ricciaceae. So if it can be shown in Ricciaceae that the intercellular space is formed by cleavage, and then splits out to the surface, the immediate reason for such distortion will have been cleared away, though it cannot be justified. Having homologized the air chamber and sex-organ pit in Ricciaceae, he applied the explanation perforce to Marchantiaceae.

Now in the case of sex-organs, it is easy to understand how the rudiment can be overgrown and left in a pit, since the growth of a whole cell line is retarded, while its neighbors surpass it. The initial at first grows more rapidly than do the adjacent cells of the thallus, the protuberance and finally the protrusion of the initial being the visible evidence of its more rapid growth. Later the adjacent cells outgrow the sex-organ and it becomes "sunk" in the thallus.

But in the matter of air chambers is involved the retardation or the cessation of growth in a very limited part of the walls belonging to four contiguous cells, while all the rest of these four walls and the remaining sixteen grow throughout, and all decidedly outgrow the lagging portion of the four! While such a thing is not impossible, it is wholly improbable and needs to be supported by most convincing evidence. Such evidence LEITGEB nowhere presents, either in text or figure. We propose to show, on the contrary, that the assumption of such peculiar lagging is unnecessary, because all the observed structures can be produced by common splitting, and the earlier stages can be produced in no other way. In presenting the evidence we have selected only a few examples, and show in the drawings merely the walls, since to show the cell contents would only obscure the essential features.

In the Ricciaceae we have examined only *Riccia fluitans* and *R. natans,* in which the origin of the air chambers is exactly alike, though the later course of development seems to be different. The origin of both is certainly by internal cleavage, and it is quite evident that the air chamber is wholly unrelated to the sex-organ pit. *Fig. 2* furnishes conclusive evidence on both points. An apical cell (?) is at *a;* at ^{1} is a young cleft and at ^{2} an older one, which has promptly broken out to the surface; while ♀ is a young archegonium. The fact that this organ is not yet overgrown by the adjacent tissues, while the air chamber ^{2} is clearly defined, shows forcibly how LEITGEB erred in homologizing the sex-organ pit and the air chamber. In *figs. 3, 4,* further stages of development are shown and also the tendency of the spaces to close at certain points, *p,* both at surface and internally by the outgrowth of cells.

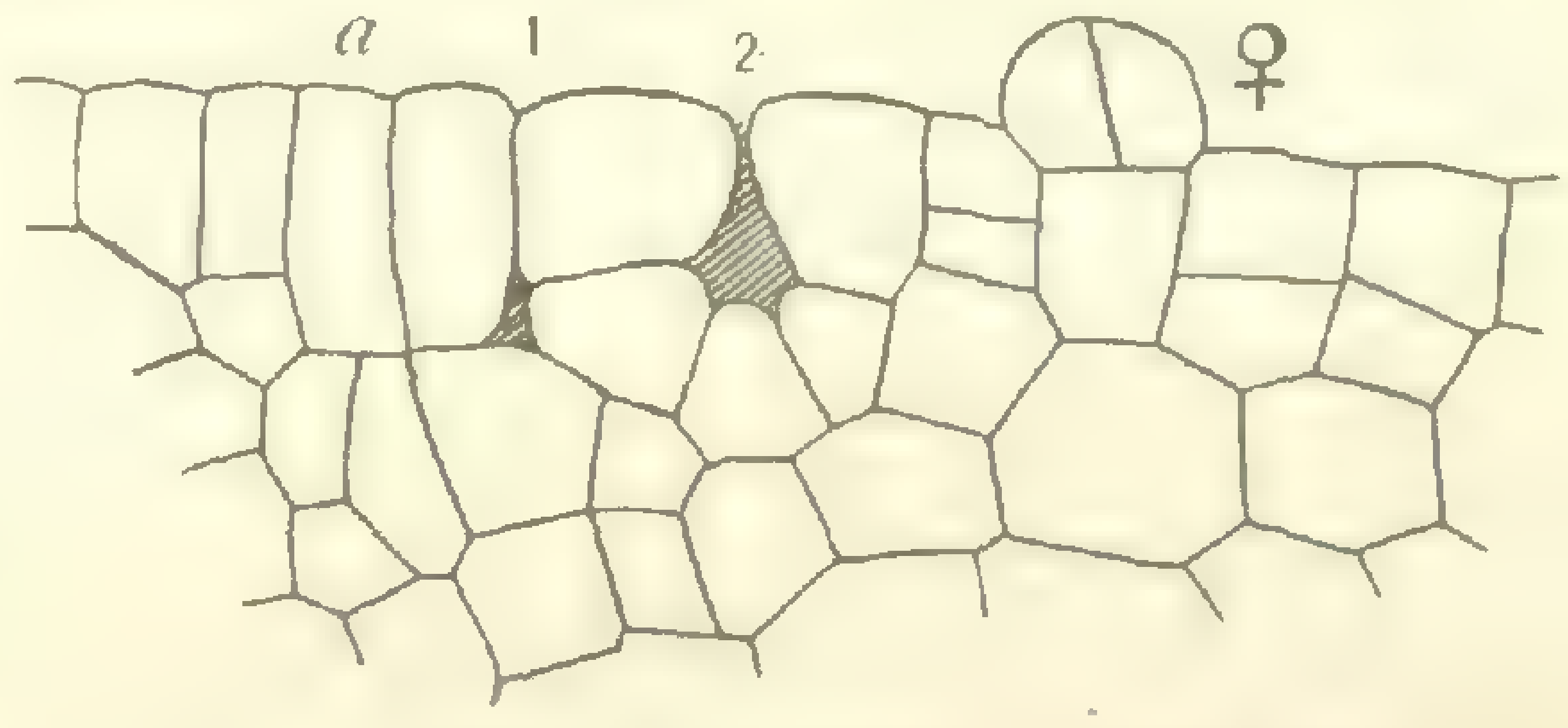

FIG. 2—*Riccia natans: a,* apical cell (?); *1, 2,* air chambers; ♀ young archegonium.

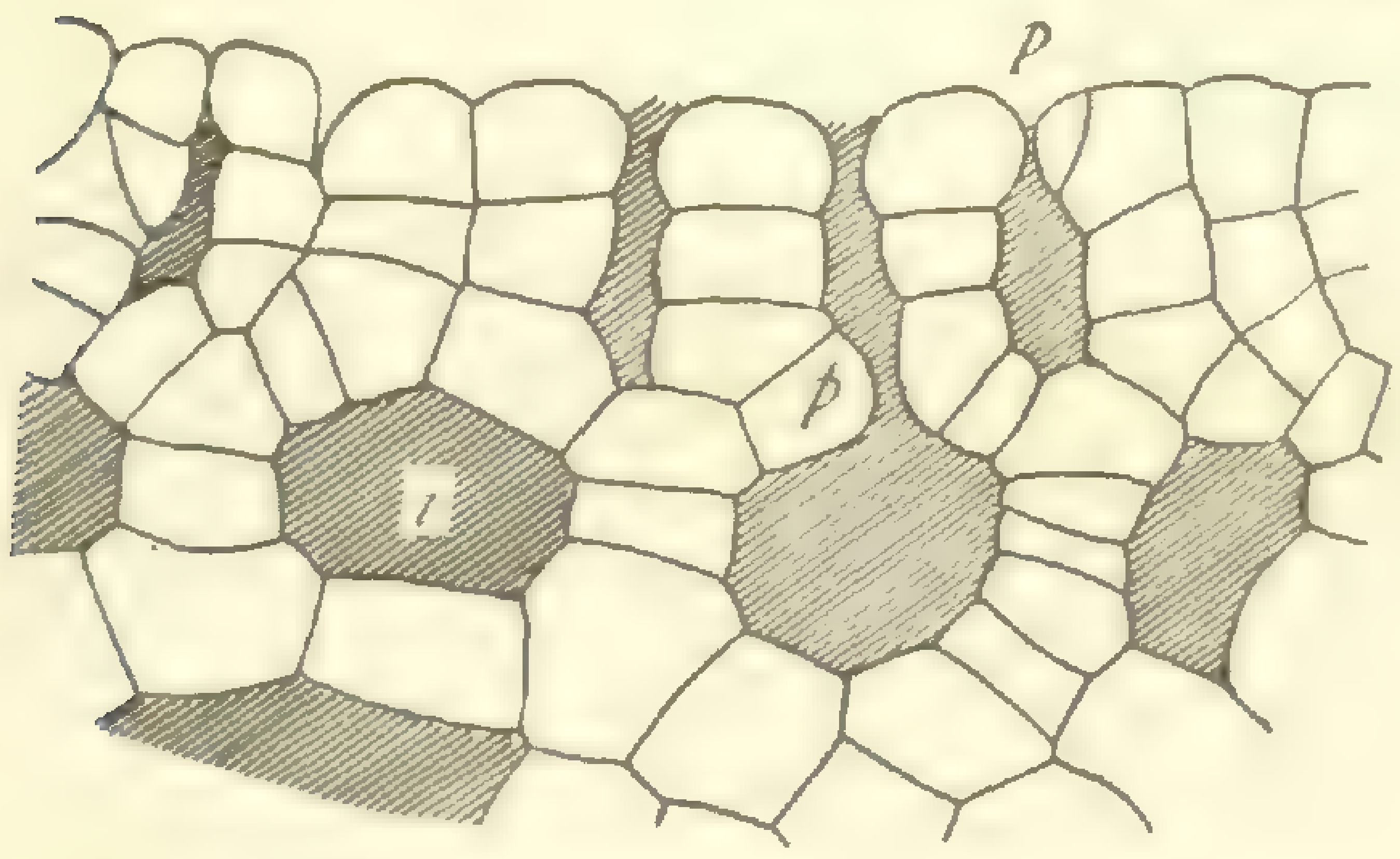

FIG. 3.—*Riccia natans.* Older air chambers; *i,* internal; at *p, p,* partial closure of passage by outgrowing cell.

The peculiar form of the thallus and the sudden tumefaction of the tissues in *Riccia natans* makes it very difficult to trace the history in detail, and we are not prepared to make any statement at present as to the later course of development of the air chambers. The system appears to be a complicated one; there is rapid enlargement of primary spaces, probably accompanied by secondary cleavage and partitioning of the chambers.

In Marchantia the splitting does not take place so early in the history of any segment and the enlargement of the intercellular spaces proceeds much more slowly. Moreover, the structure of the thallus makes it easier to secure sections through the apical region, so that one may readily observe the origin and follow the development of the air chamber. It seems probable from our observations that the time and place of the first splitting is somewhat variable, depending upon the relation between cell division and enlargement.

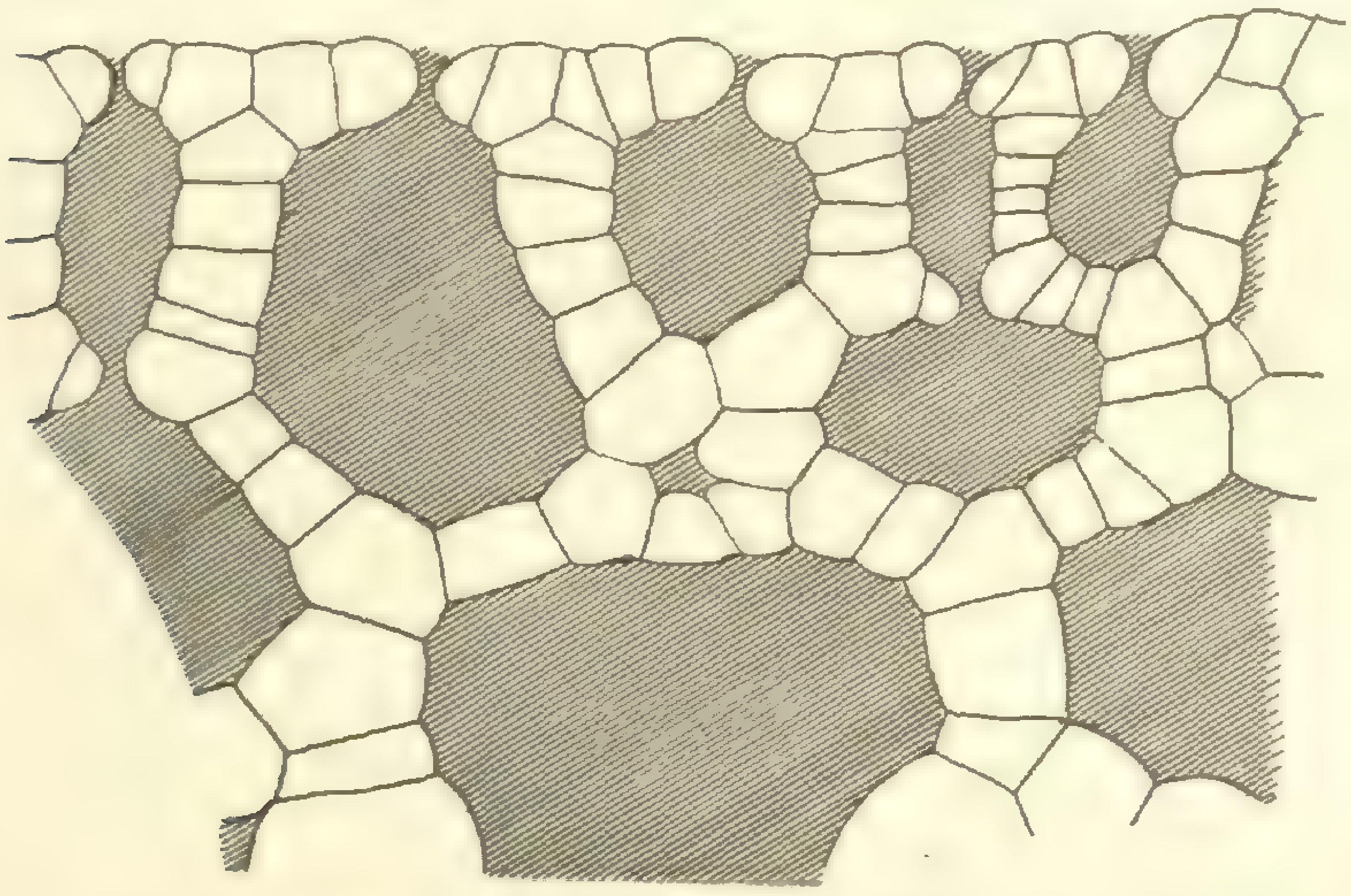

FIG. 4.—*Riccia natans.* Nearly mature air chambers, superficial and internal, primary and secondary.

The normal position of the cleft is either in the center of a segment of the apical cell near the surface or in the center of one or another of its primary surface segments formed by a further dvision. A periclinal division of the segment may cut it into a superficial and an internal cell. This superficial cell is oftenest the mother cell of the chamber (*fig. 9*). Then two anticlinal walls, ^{2} ^{2}, and another, ^{3}, in the plane of the drawing, divide this "mother cell" into four, a dextral and sinistral, an anterior and

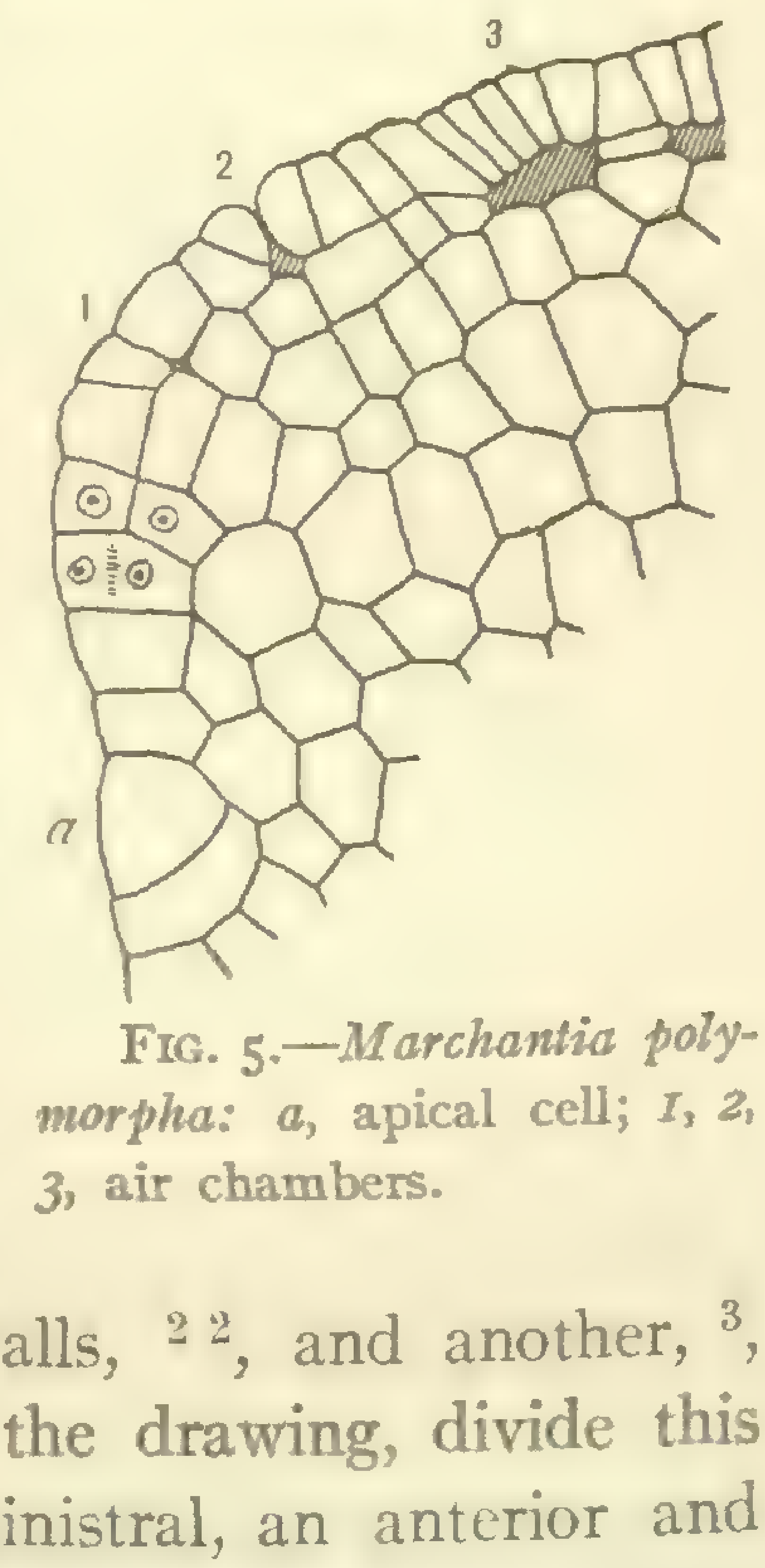

FIG. 5.—*Marchantia polymorpha: a,* apical cell; *1, 2, 3,* air chambers.

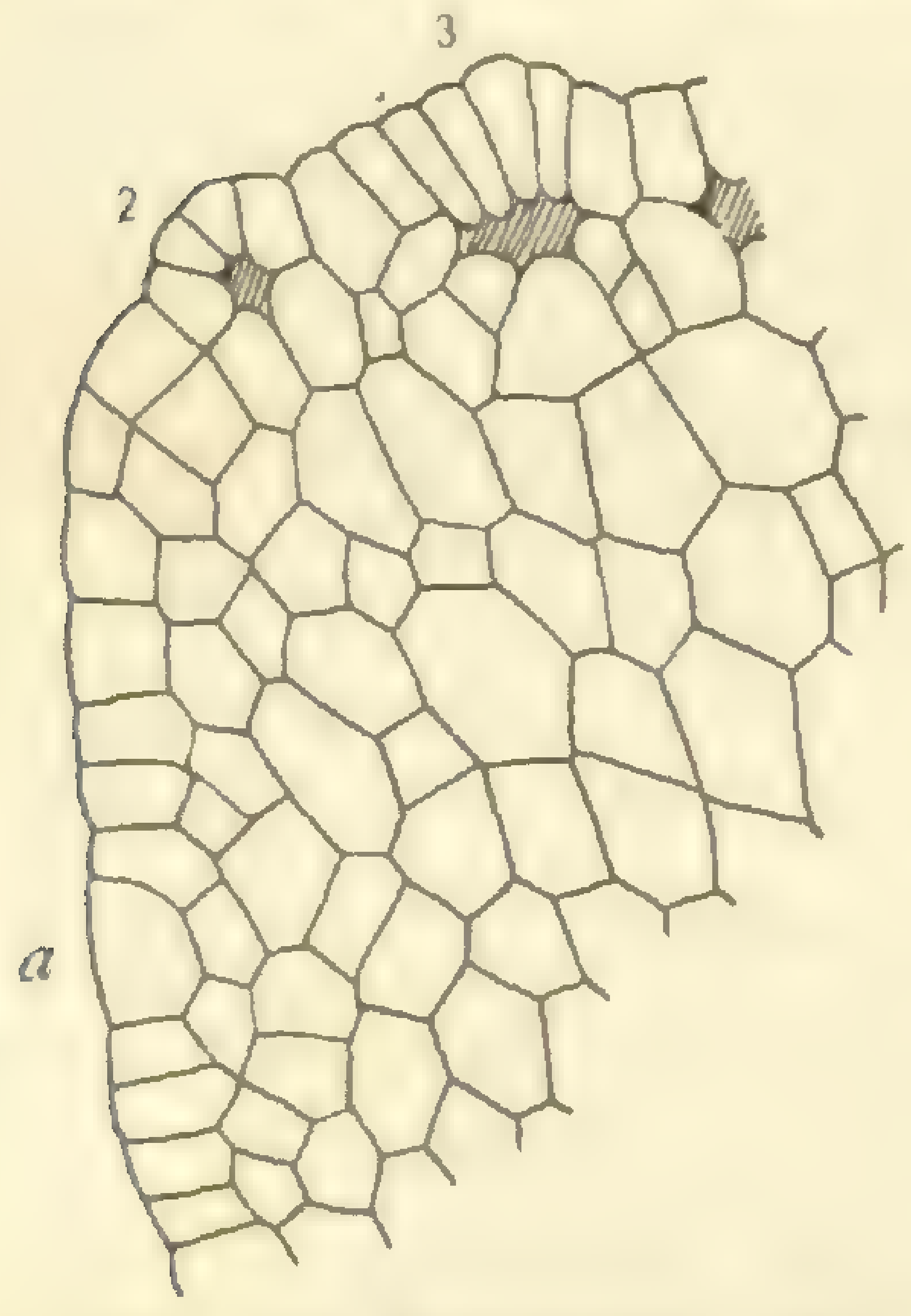

FIG. 6.—*Marchantia polymorpha: a,* apical cell; *2, 3,* air chambers.

a posterior cell. Each is then divided, in the plane ^{4} ^{4}, into a superficial and an internal cell by a periclinal division, and at the intersection of these last walls with the preceding anticlinal one, ^{2} ^{2}, the split usually occurs. This is promptly followed by divisions, ^{5} ^{5}, to form the cells of pore margin and roof. In *fig. 5* the four nuclei mark the place of the split; for were the division in progress completed, the cleft would appear at the corner common to these four cells.

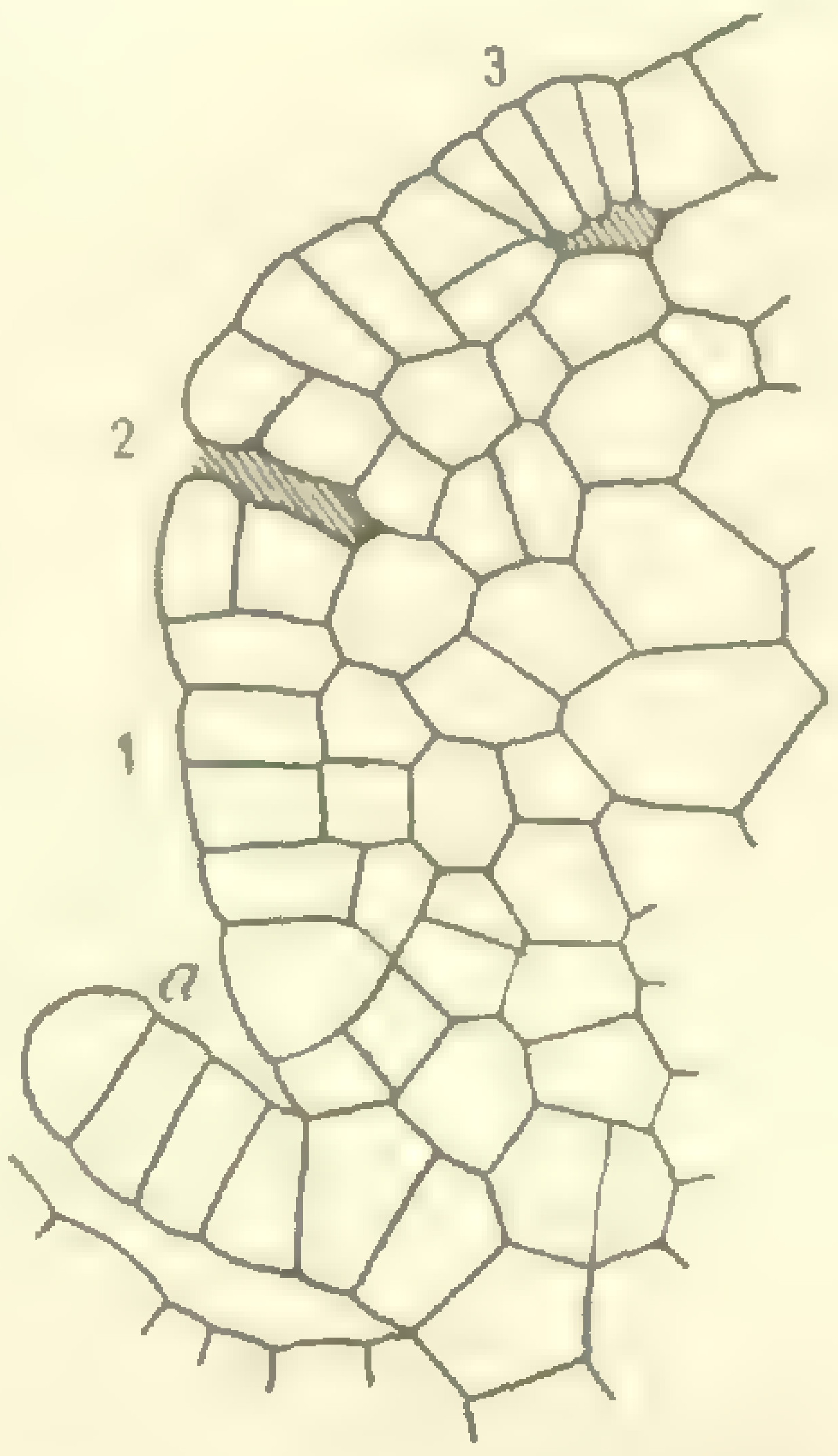

FIG. 7.—*Marchantia polymorpha: a*, apical cell; *2, 3*, air chambers; at *1* the next one is due after division of outer cells.

There is also more or less variation in the course of development. Sometimes the nascent chamber breaks out to the surface and remains wide open for a time (*fig. 7*, ^{2}); sometimes (and more commonly) divisions ensue so promptly in the cells above the primary cleft that the turgor of the newly formed cells keeps the passage closed from the beginning (*figs. 6*, ^{3}; *8*, ^{1,2}). These quickly divide (*figs. 6*, ^{3}; *7*, ^{3}; *9*) and by repeated divisions give rise to the roof and the pore margin (*fig. 10*) of the well-known form.

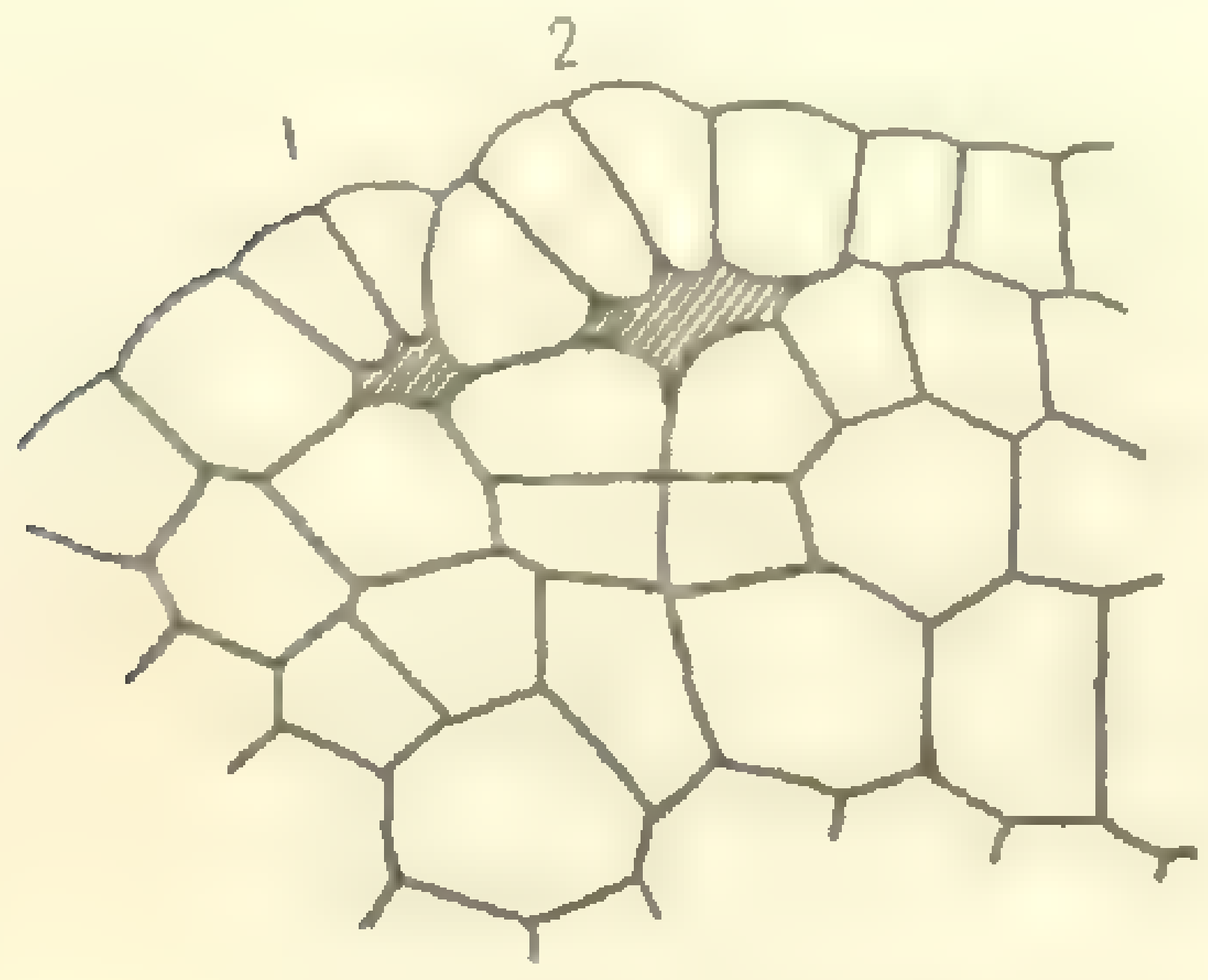

FIG. 8.—*Marchantia polymorpha: 1, 2*, air chambers; *2* shows tardy division of roof cells.

A comparison of these figures with *fig. 17, plate 12*, of LEITGEB'S *Untersuchungen*, and the earlier figures of his paper on the stomata of Marchantia (*l. c.*, footnote 3), shows clearly enough that he saw essentially similar stages, though probably not such early ones as we indicate. It was chiefly in the interpretation of his observations that he went astray.

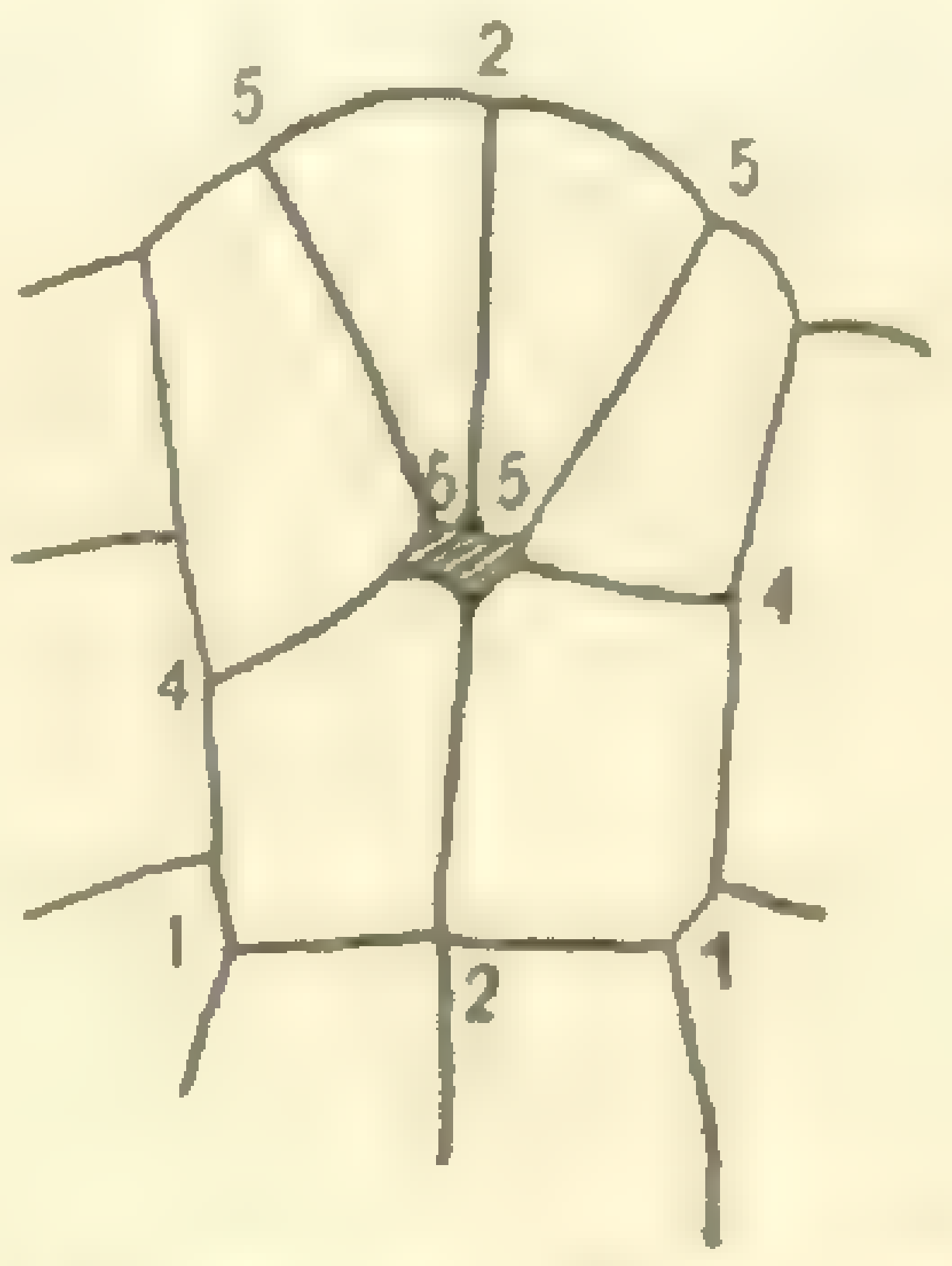

FIG. 9.—*Marchantia polymorpha*. Diagram of the course of normal division of the "mother cell" of an air chamber; the numbers show the sequence of walls.

In Lunularia the process is similar in all respects to that in Marchantia, though the material available was not as vigorous as could have been desired. The splitting is prompt and the divisions follow so quickly that the roof and cells of the pore margin are soon completed (*fig. 11*).

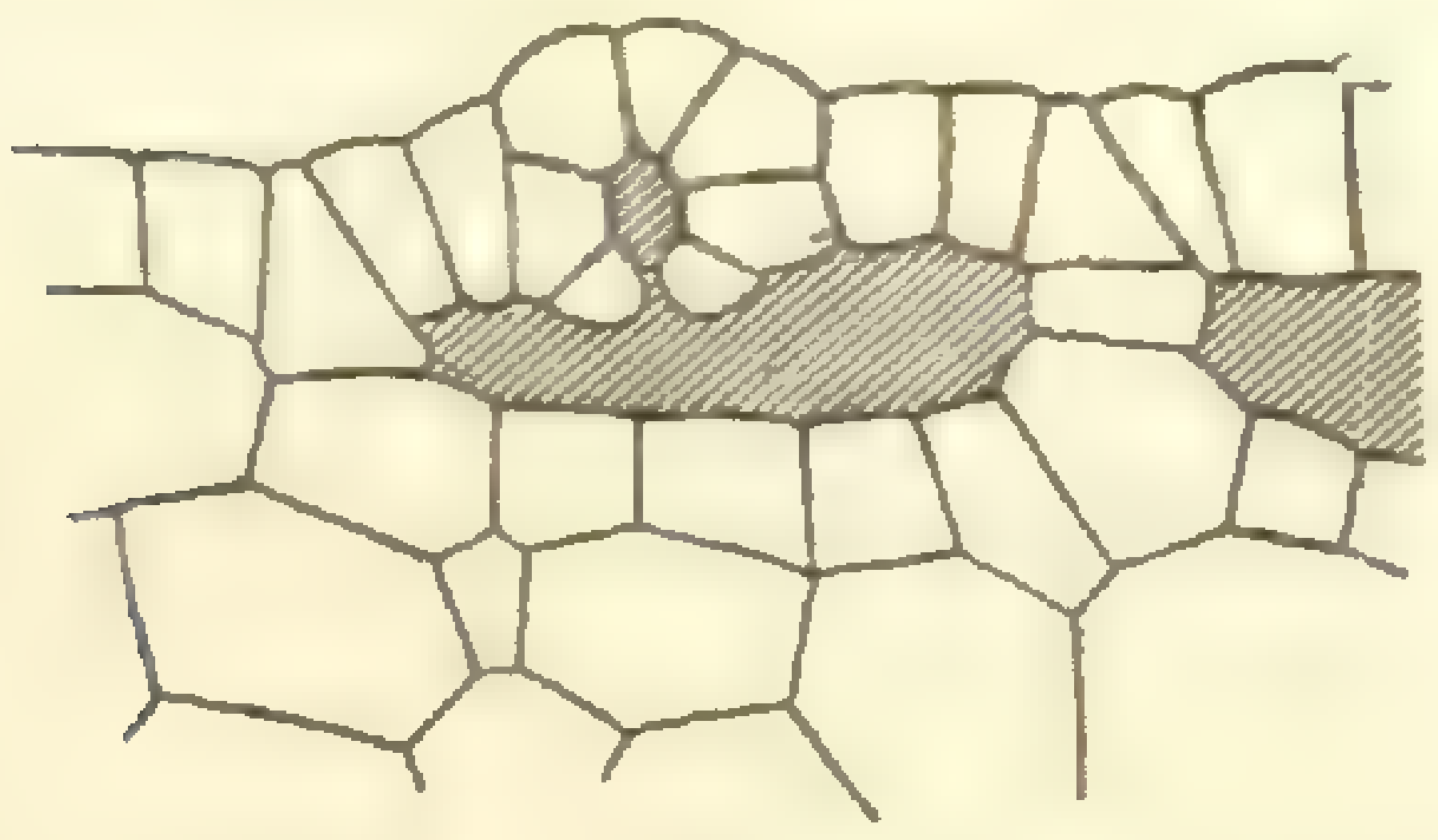

FIG. 10.—*Marchantia polymorpha.* Formation of the pore margin, with complete closure.

In Conocephalus also the formation of the air chamber is rapid (*figs. 12, 13*) and the details are not as regular and therefore not as easy to follow as the Marchantia. After the initial cleft has extended to the surface (*fig. 12,* ^{2}) the expansion of the tissues at first outstrips the divisions which are to produce the roof, so that the chamber is open (*fig. 12,* ^{3,4}, *fig. 13,* ^{3,4}). Later the roof closes the chamber, perhaps intermittently (*fig. 12,* ^{5}, *fig. 13,* ^{4,6}), which only becomes permanently open when the divisions for the pore margin begin (*fig. 13,* ^{6,7}).

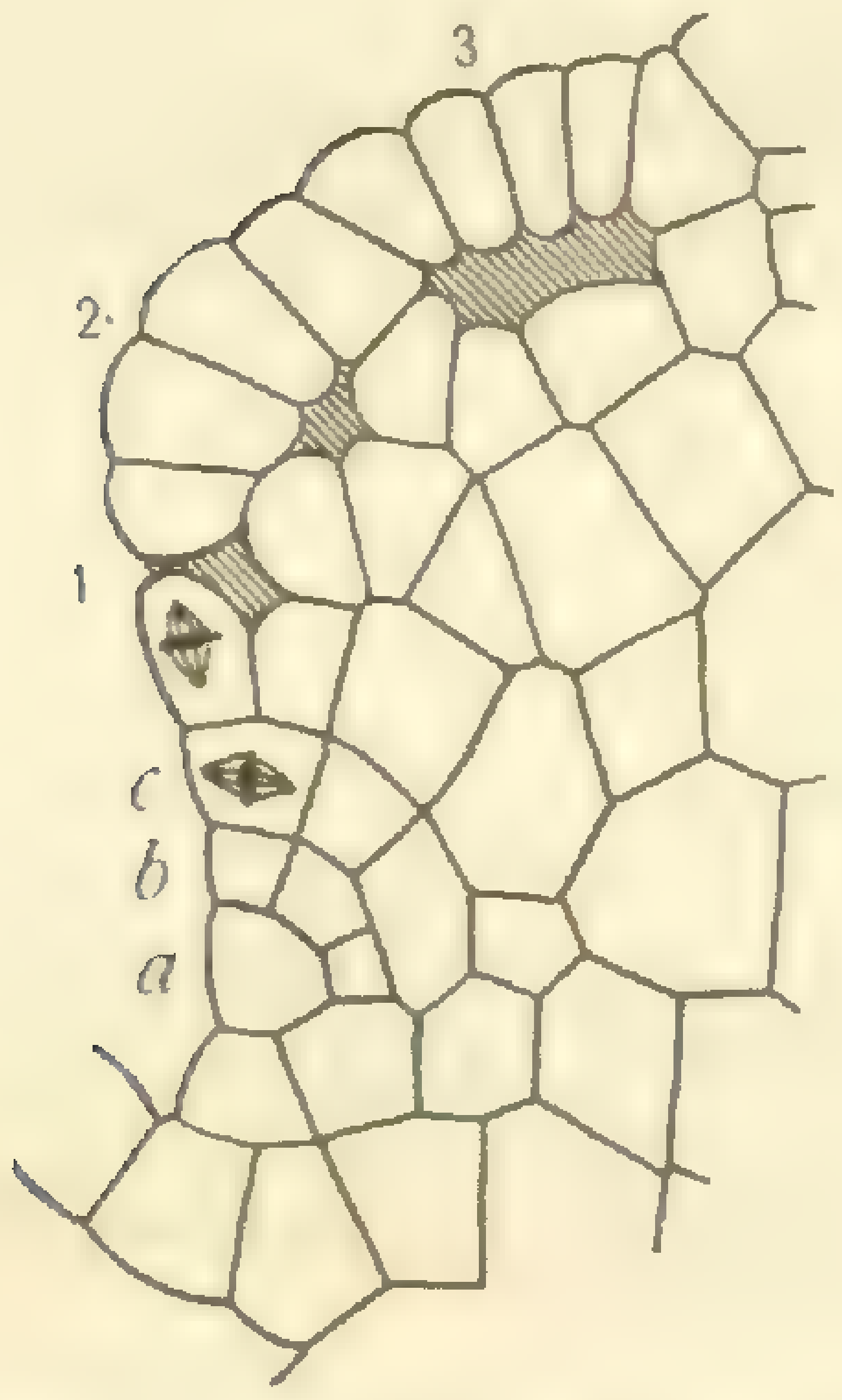

FIG. 11.—*Lunularia vulgaris: a,* apical cell; *b, c,* successive segments; *1, 2, 3,* air chambers.

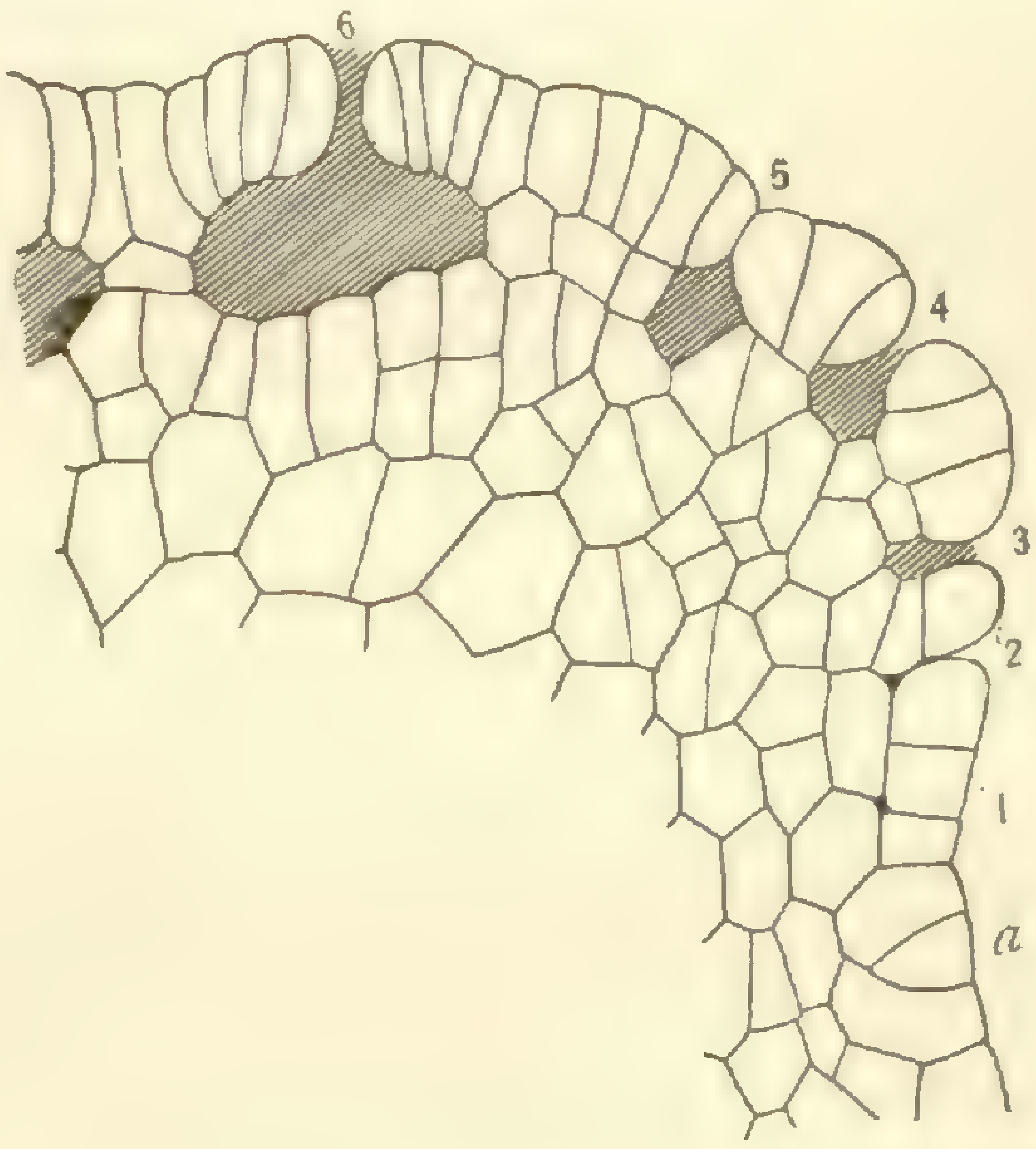

FIG. 12.—*Conocephalus conicus: a,* apical cell; *1–6,* air chambers.

Dumortiera (*figs. 14, 15*) forms air chambers that later disappear more or less completely, leaving only traces of their rhomboidal outlines on the surface.[11] The plants grow in very damp places, and all the tissues concerned with the formation of air chambers have an oedematous look, being soon greatly swollen, with scanty contents.

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[11] CAMPBELL found no evidence of air chambers in *D. trichocephala,* which we have not seen. It would be very remarkable if the early stages were wholly wanting.

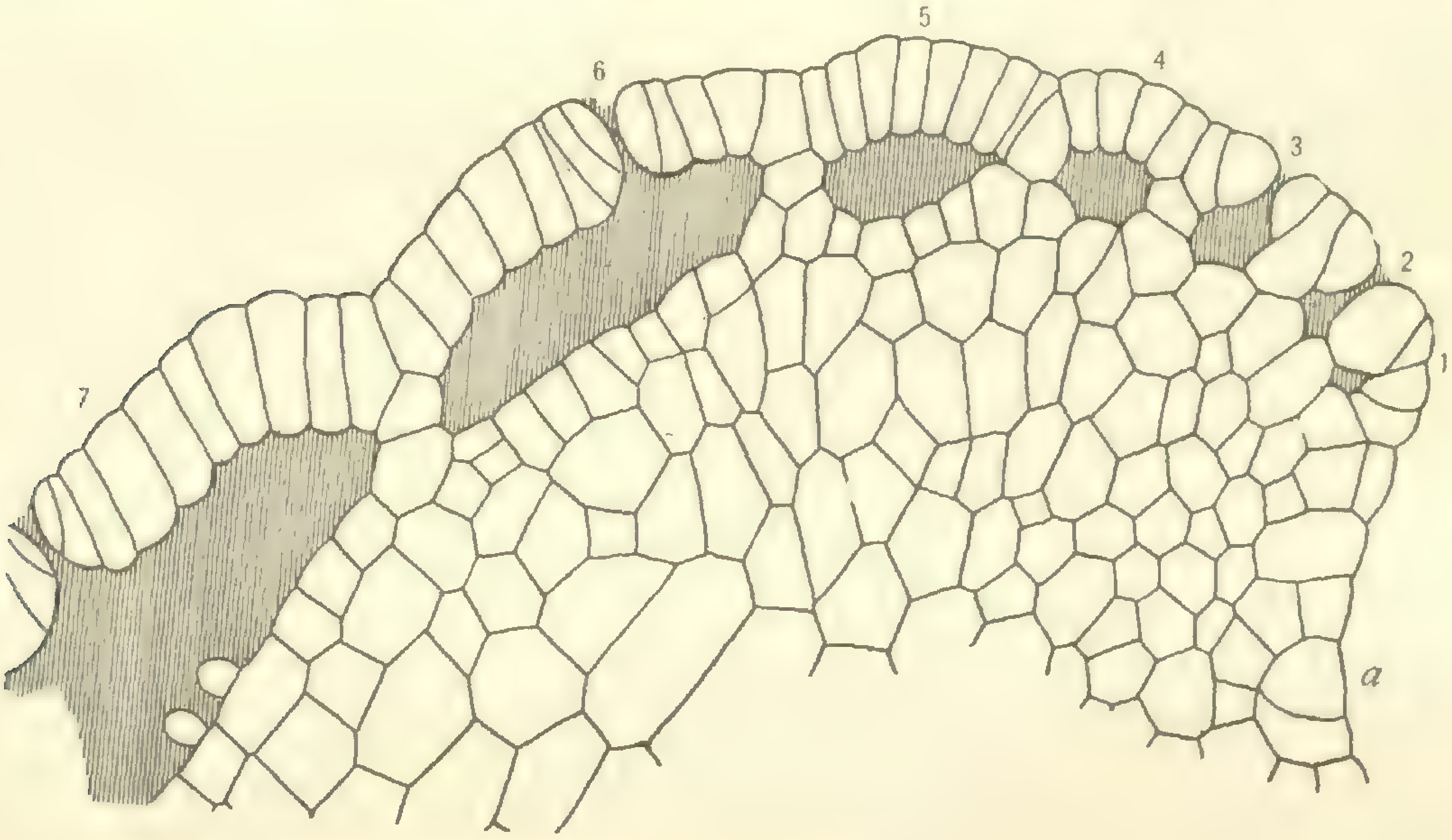

FIG. 13.—*Conocephalus conicus: a*, apical cell; *1–7*, air chambers.

In consequence of the excessive turgor, apparently, the splitting is very prompt and complete, so that the young internal space is difficult to find. The air chambers develop rapidly, and "blow up," so to speak, within a short distance of the apex, only the ragged walls and roofs, in section like a letter Y, remaining for a time.

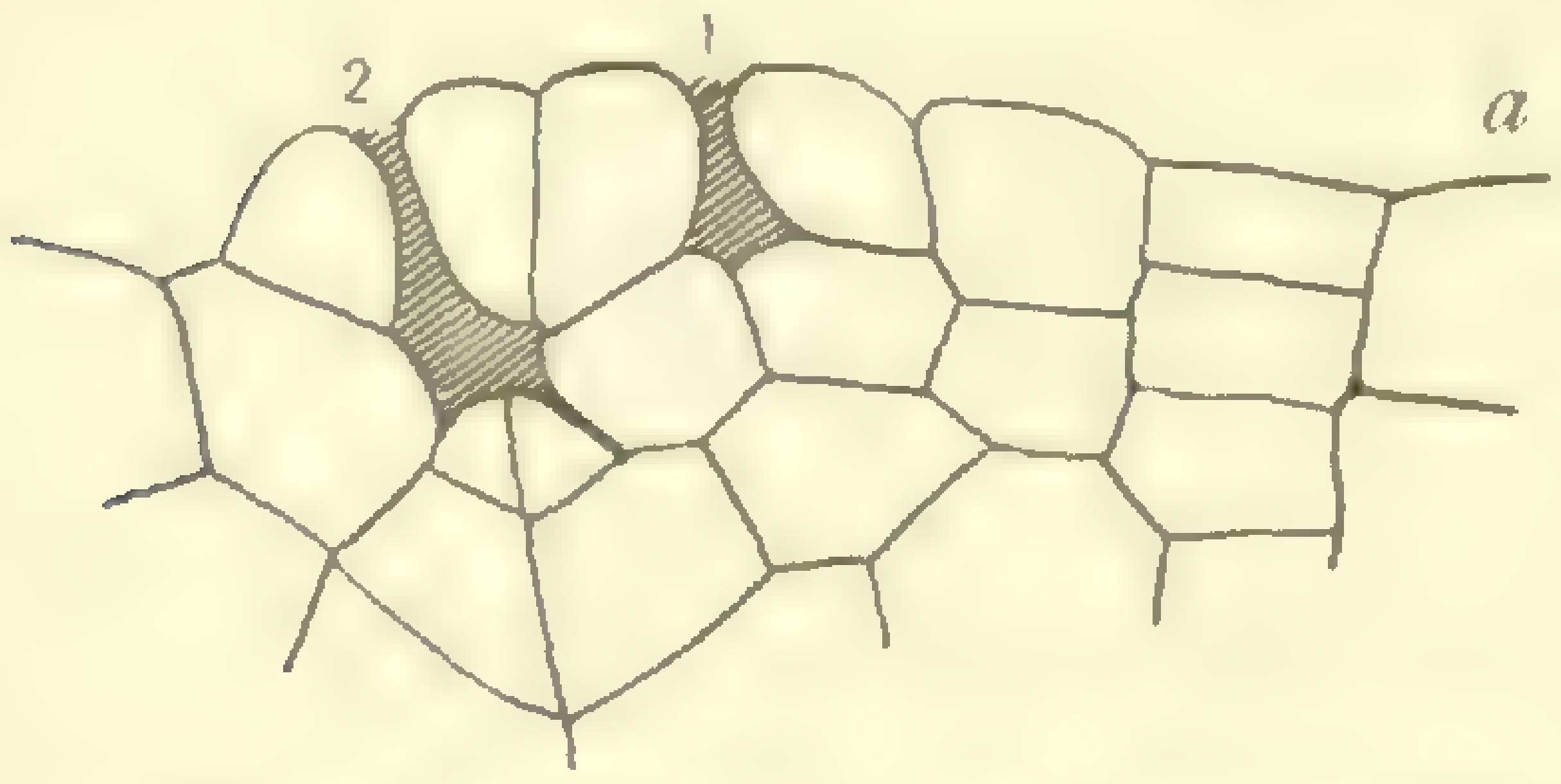

FIG. 14.—*Dumortiera hispida* (?): *a*, apical region; *1, 2*, air chambers.

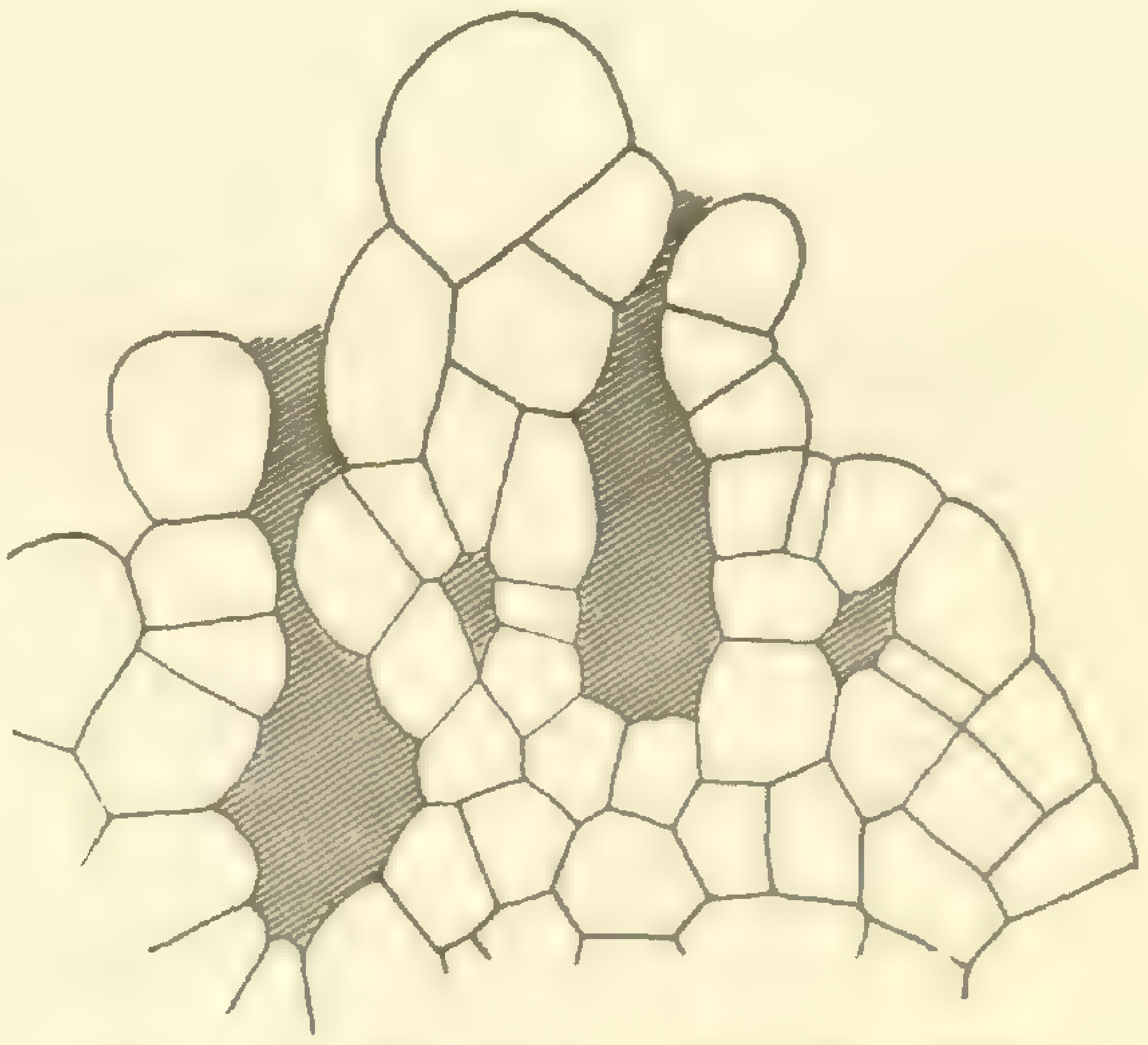

FIG. 15.—*Dumortiera hispida*. Older air chambers, deformed by excessive turgor.

It will be observed that the air-chamber region in Marchantia, Lunularia, Conocephalus, and Dumortiera is superficial. By no means all of the tissues arising from the dorsal segments of the apical cell show splitting, but much the greater part is compact, with no intercellular spaces of any kind. In Fimbriaria and Plagiochasma, however, the splitting involves all the tissue which arises from the dorsal segments of the apical cell, so that a much greater part of the thallus is permeated by extensive and irregular air passages (*fig. 16*), which make it almost as spongy as Ricciocarpus.

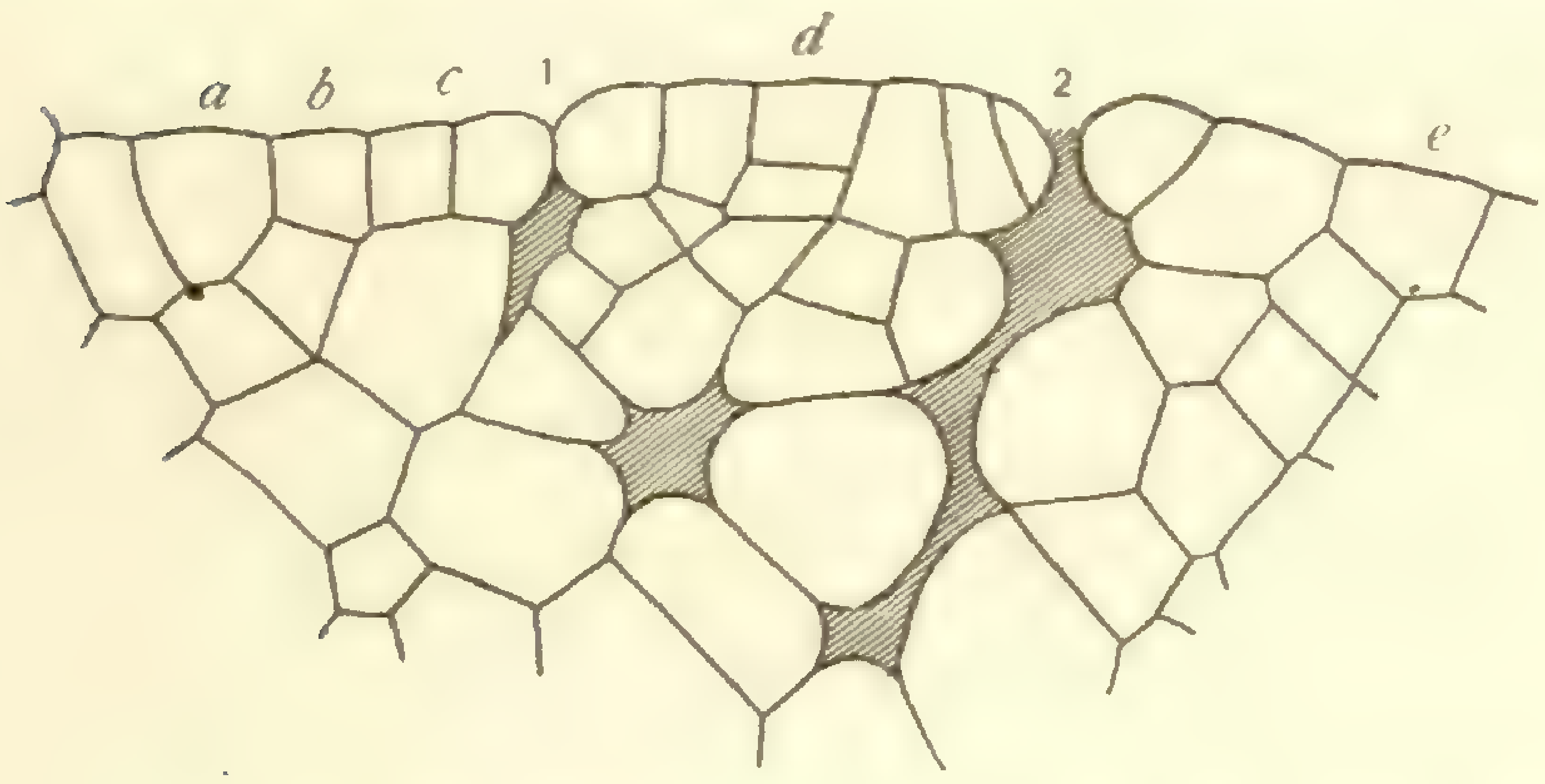

FIG. 16.—*Fimbriaria echinella: a*, apical cell; *b–e*, successive segments; *1, 2*, air chambers; in *d* a secondary deep-seated cleft.

In Fimbriaria the primary splitting usually begins between the cells arising from successive segments (*fig. 16*, 1, 2, where 1 lies between segments *c* and *d*, and 2 between *d* and *e*). Later, and often deep in the tissue, secondary splitting gives rise to intercellular spaces which may reach the surface or may break into a primary space.

In Plagiochasma the splitting is likewise more pronounced between the offspring of different segments (*fig. 17*), but the secondary splitting, if such it may be called, occurs so promptly and becomes so extensive as to be hardly distinguishable from the primary (*figs. 18, 19*, 3a, 4a). The air passages are open almost or quite uninterruptedly until the pore margin is well begun (*fig. 20*). There is never a wide and shallow chamber, over whose increasing area a roof forms, *pari passu;*

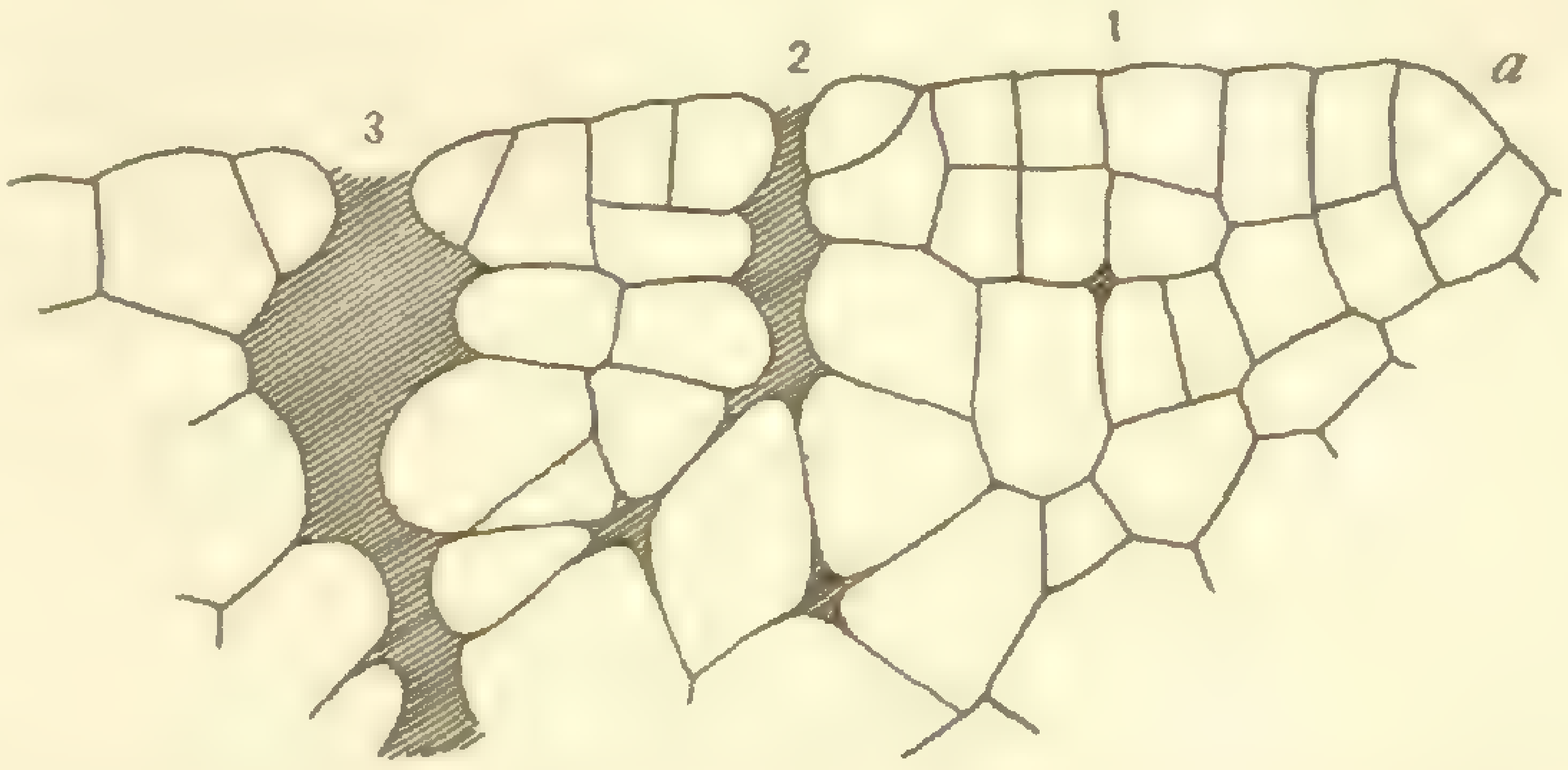

FIG. 17.—*Plagiochasma* sp: *a*, apical cell; *1–3*, air chambers.

but the passages are always deep and narrow, with hardly more than the pore margin for a roof (*fig. 21*). There are many spaces near the surface which have no direct opening by pore (*fig. 22, c*). These connect doubtless with the spaces that do have pores (*fig. 22, o*). Whether partitioning of the chambers occurs, as described by LEITGEB, by the outgrowth of cell plates in Plagiochasma and in Ricciocarpus, we have not fully determined, though it appears probable; but the

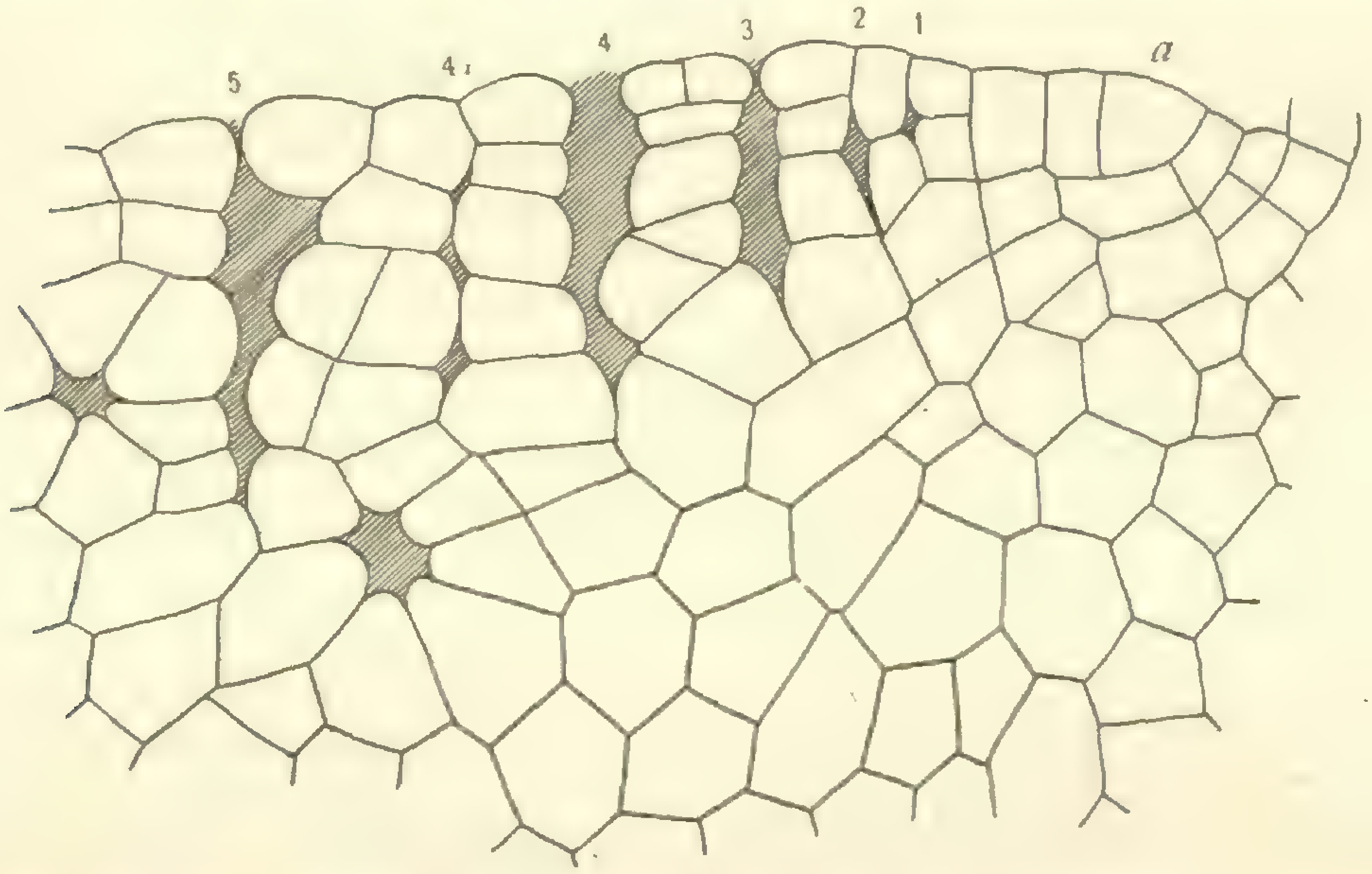

FIG. 18.—*Plagiochasma* sp.: *a*, apical cell; *1–5*, air chambers; *4a* secondary splitting between primary clefts *4, 5*.

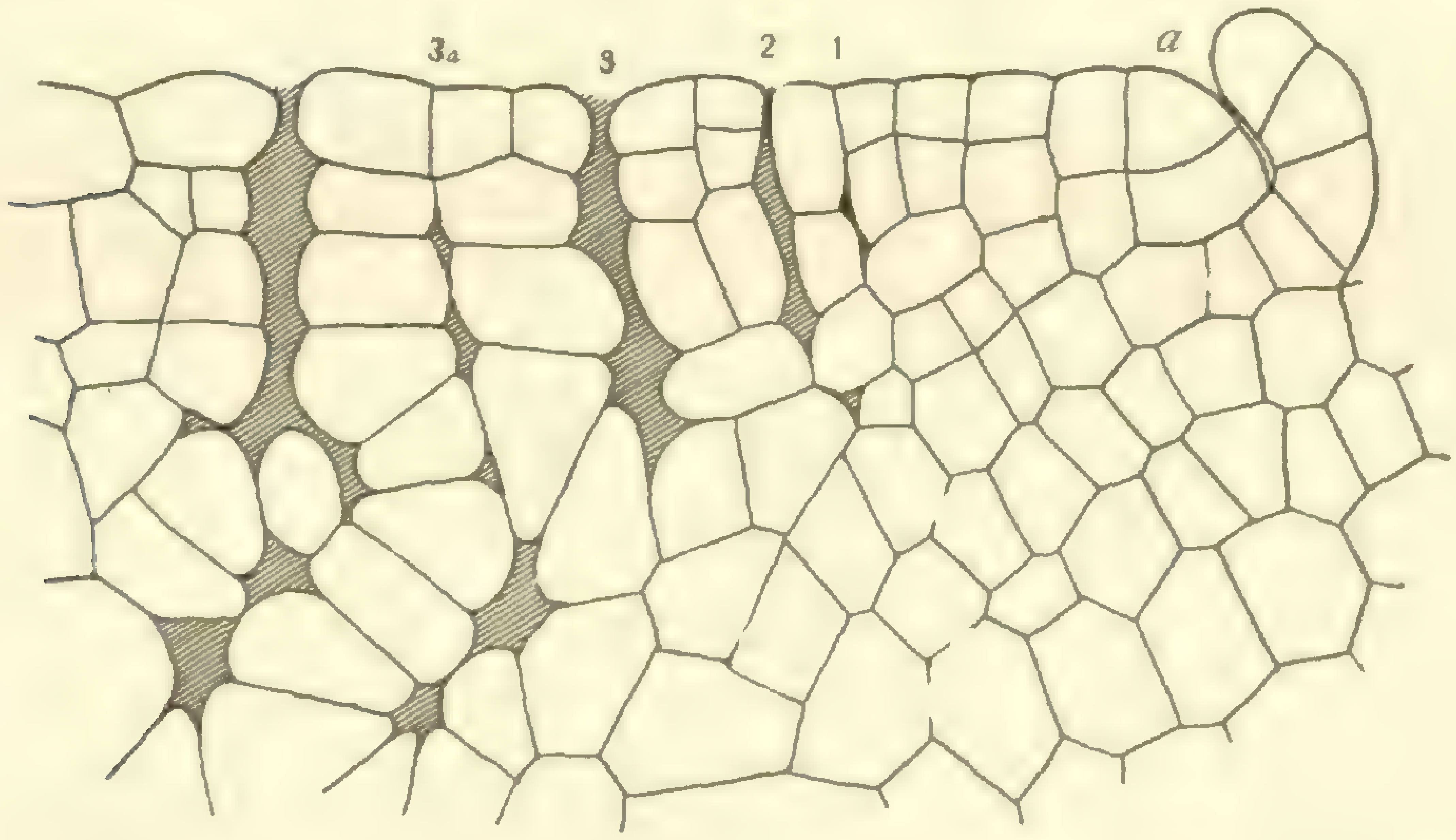

FIG. 19.—*Plagiochasma* sp.: *a*, apical cell; *1–4*, air chambers; *3a*, secondary splitting.

formation of the aerating system is mainly due to splitting and growth.

How LEITGEB discounted the evidence of his eyes is well shown in the case of Plagiochasma, in which he saw and figured intercellular spaces,[12] as to which he remarks:[13]

> In *P. Aitonia* they (the air chambers) appear in both longitudinal and cross-sections very commonly in the form of extremely small intercellular spaces, like those in ordinary parenchyma, and *one could scarcely dismiss the idea that they are formed by cleavage in originally compact tissue,* did not corresponding relations in other species speak against this interpretation.

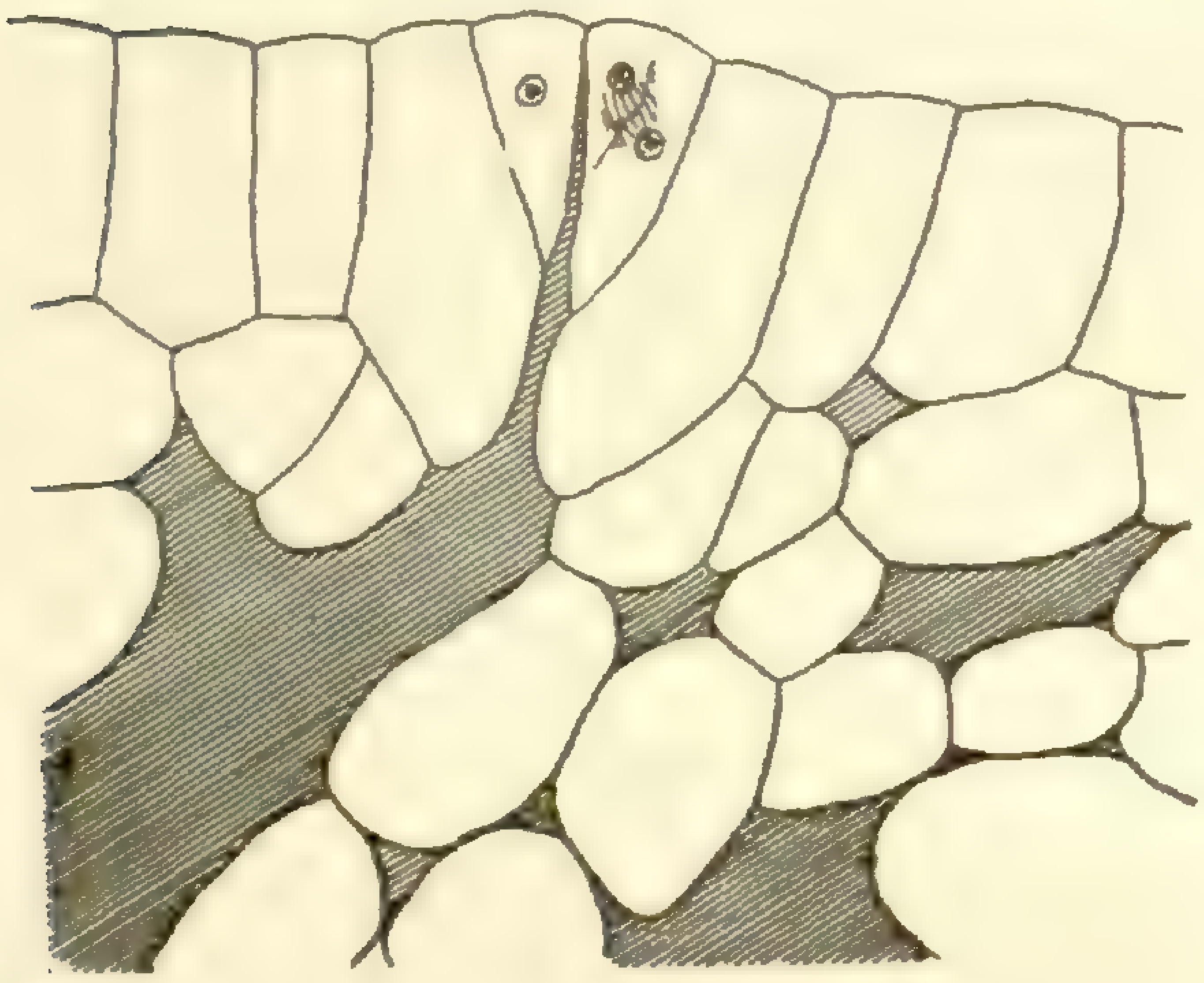

FIG. 20.—*Plagiochasma* sp. Beginning of pore margin.

As a matter of fact, corresponding relations in other species do not speak against this interpretation, but confirm it.

Finally we may point out that, instead of homologizing the formation of the air chambers in Marchantiales with the formation of sex-organ pits, which it required considerable distortion of the facts to do, we have brought their origin into line with the much more

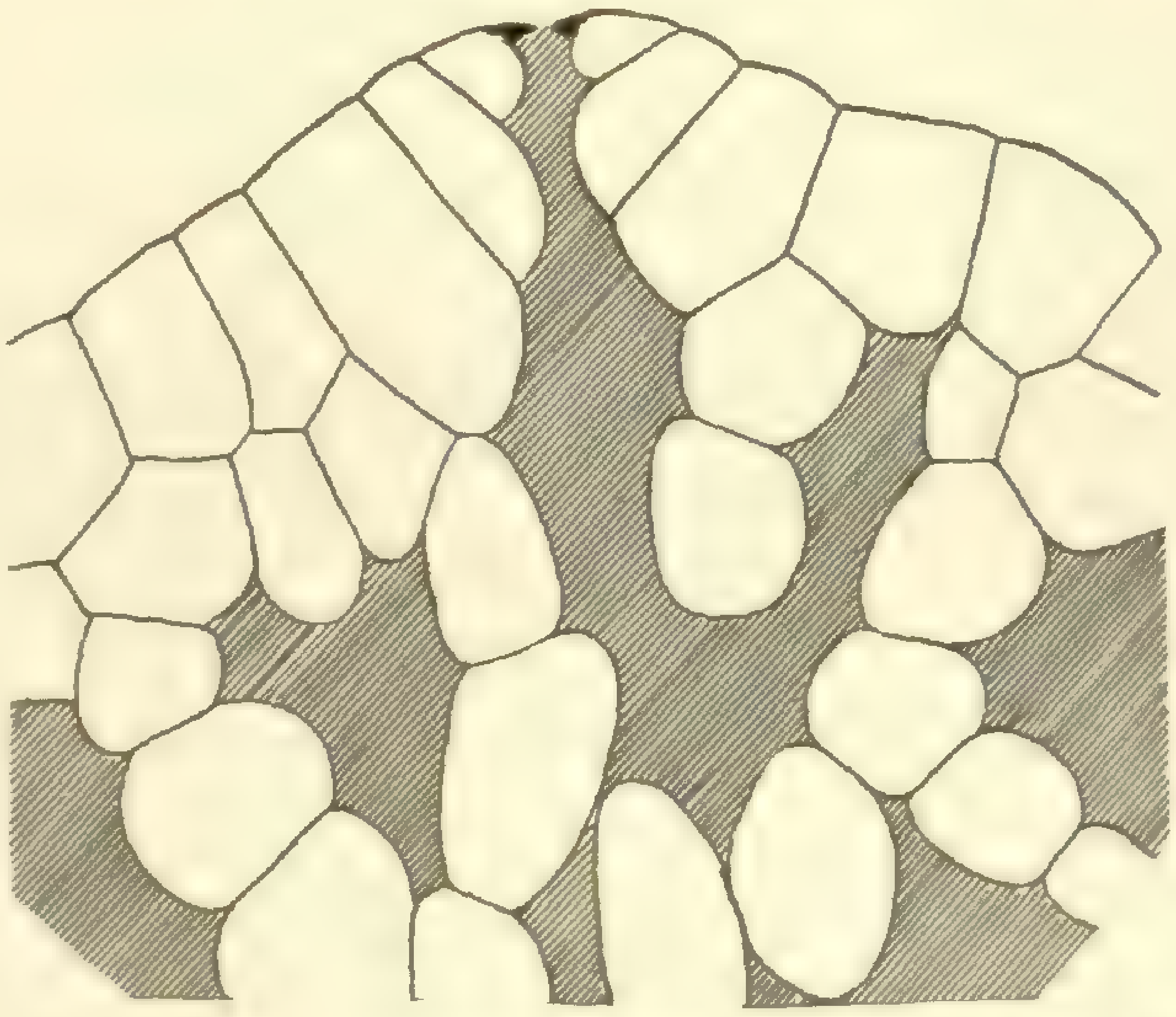

FIG. 21.—*Plagiochasma* sp. Pore margin complete.

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[12] Untersuchungen über der Lebermoose **6**: *pl. 1. fig. 4.*

[13] Bei *Pl. Aitonia* erscheinen dieselben an Längs- wie Querschnitten sehr häufig in Form äusserst kleiner Intercellularräume, wie sie im gewöhnlichen Parenchym vorkommen und man könnte die Annahme, sie entständen durch Spaltungen in ursprünglichem fest gefugtem Gewebe, kaum von der Hand weissen, wenn nicht die entsprechenden Verhältnisse bei den übrigen Arten gegen diese Deutung sprechen würden.—*l. c.*, p. 64.

general phenomenon, the formation of schizogenous intercellular spaces.

Our conclusions may be summarily stated thus: The air chambers of Marchantiales arise invariably by the splitting of internal cell walls, usually at the junction of the outermost and first internal layer of cells. Thence, in one type splitting proceeds outwardly and inwardly more extensively than laterally, and lateral enlargement of the chamber follows by growth; while in the other type expansion of the chamber is due to extensive inward splitting accompanied by growth. The origin of the air chamber is in all respects like that of intercellular spaces in the vascular plants.

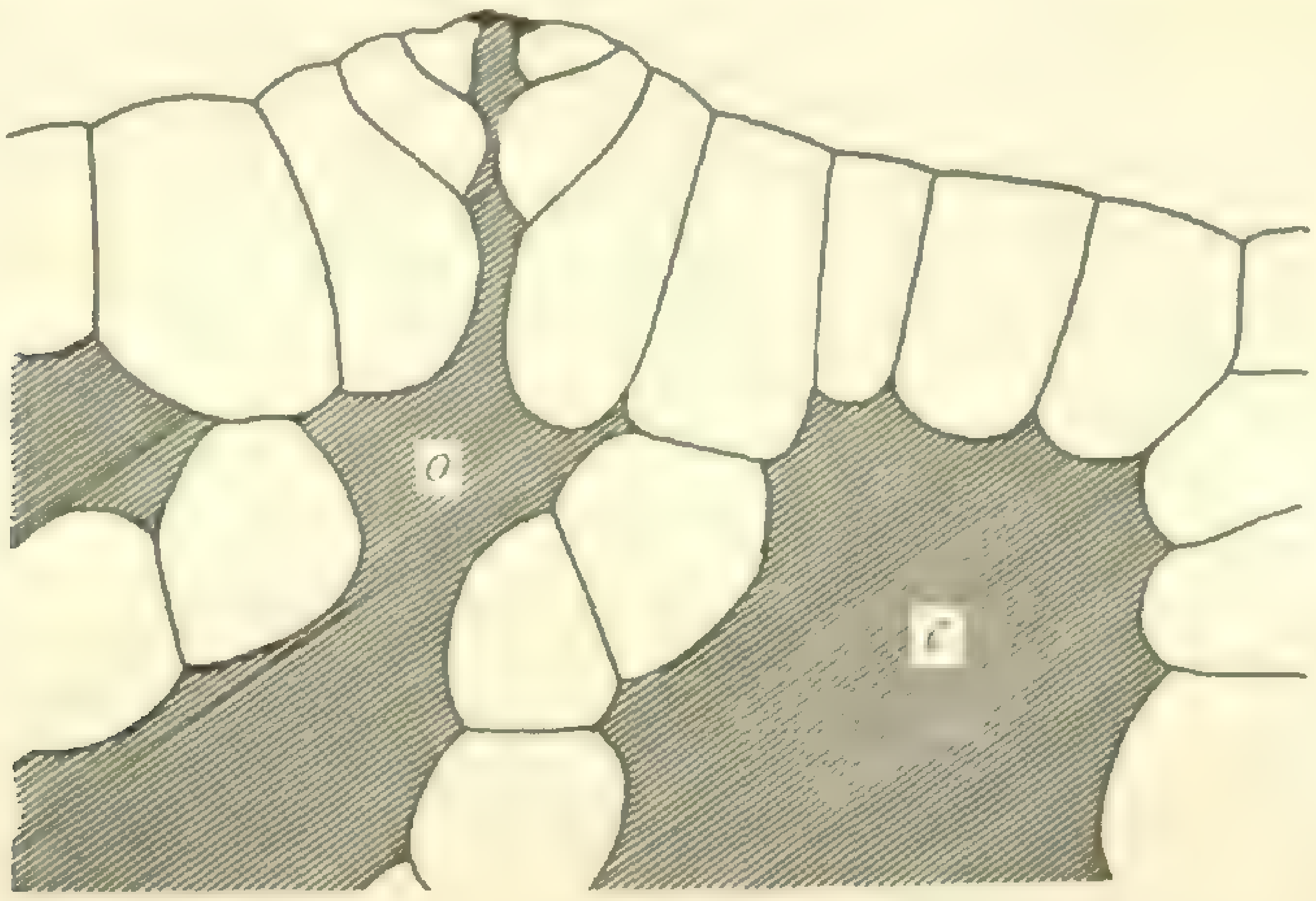

FIG. 22.—*Plagiochasma* sp.: *o*, air chamber opening through pore; *c*, closed chamber.

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NOTE.—The figures are all drawn to the same scale and appear here magnified about 550 diameters.

THE DEVELOPMENT OF THE SPORANGIUM OF LYGODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, 101

R. BINFORD

(WITH THIRTY-SEVEN FIGURES)

In his "Studies in the morphology of spore-producing members" (No. IV), BOWER suggests a line of evolution from the Marattiaceae to the Polypodiaceae, with the Osmundaceae, Schizaeaceae, Gleicheniaceae, Cyatheaceae, Hymenophyllaceae, and related forms as representatives of intermediate types. The Marattiaceae and Polypodiaceae are well-worked groups, but the intermediate forms are not so well known. Lygodium, one of the Schizaeaceae, has been chosen, therefore, for the present study.

In his classical work on this family, PRANTL[1] considered the morphology and the taxonomy of the whole family. His description of the sporangium of Lygodium is here verified except in one point, which will be mentioned later. The present work calls attention to some points that have not been noted in other studies and emphasizes some that have been quite neglected.

The material of the present study came from the Philippine Islands and was collected by Dr. H. N. WHITFORD on Mount Mariveles, Province of Bataan, Luzon, and was sent to the University of Chicago for demonstration purposes. The species described in the paper is *L. circinatum;* but *L. flexuosum* was also examined and found to be somewhat less variable.

ARRANGEMENT AND ORDER OF SPORANGIA.—The sporangia are in two rows on the ventral surface of the fertile lacinia, and are solitary, i. e., there is only one sporangium in a sorus; PRANTL calls this a "monangial" sorus. The indusium grows out around the sporangium so as to form a pocket open toward the apex on the ventral side of the leaf (*figs. 1, 2*). The sporangia arise in acropetal succession on the margin of the lacinia (*fig. 3*). The initial cell of the sporangium appears as a marginal cell near the apex of the pinnule; and at first it projects obliquely outward and forward. The indusium arises from the edge and ventral surface of the pinnule basal to the sporangium (*fig. 4*). The growth of the indusium out from the edge of the pinnule carries the base of the sporangium out, as shown in *fig. 3*, so that it projects forward or slightly in toward the costa. The part of the indusium which arises from the ventral surface grows out and forward so as to cover the sporangium on the ventral side, but on the dorsal side it is exposed for some time (*figs. 5, 6*). Later a forward growth of lamina incloses the sporangium (*fig. 3*), and carries its base forward so that it projects in a ventral direction. It has thus been

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[1] Untersuchungen zur Morphologie der Gefässkryptogamen. 2. Heft. Die Schizaeaceen, morphologisch und systematisch bearbeitet. Leipzig. 1881.

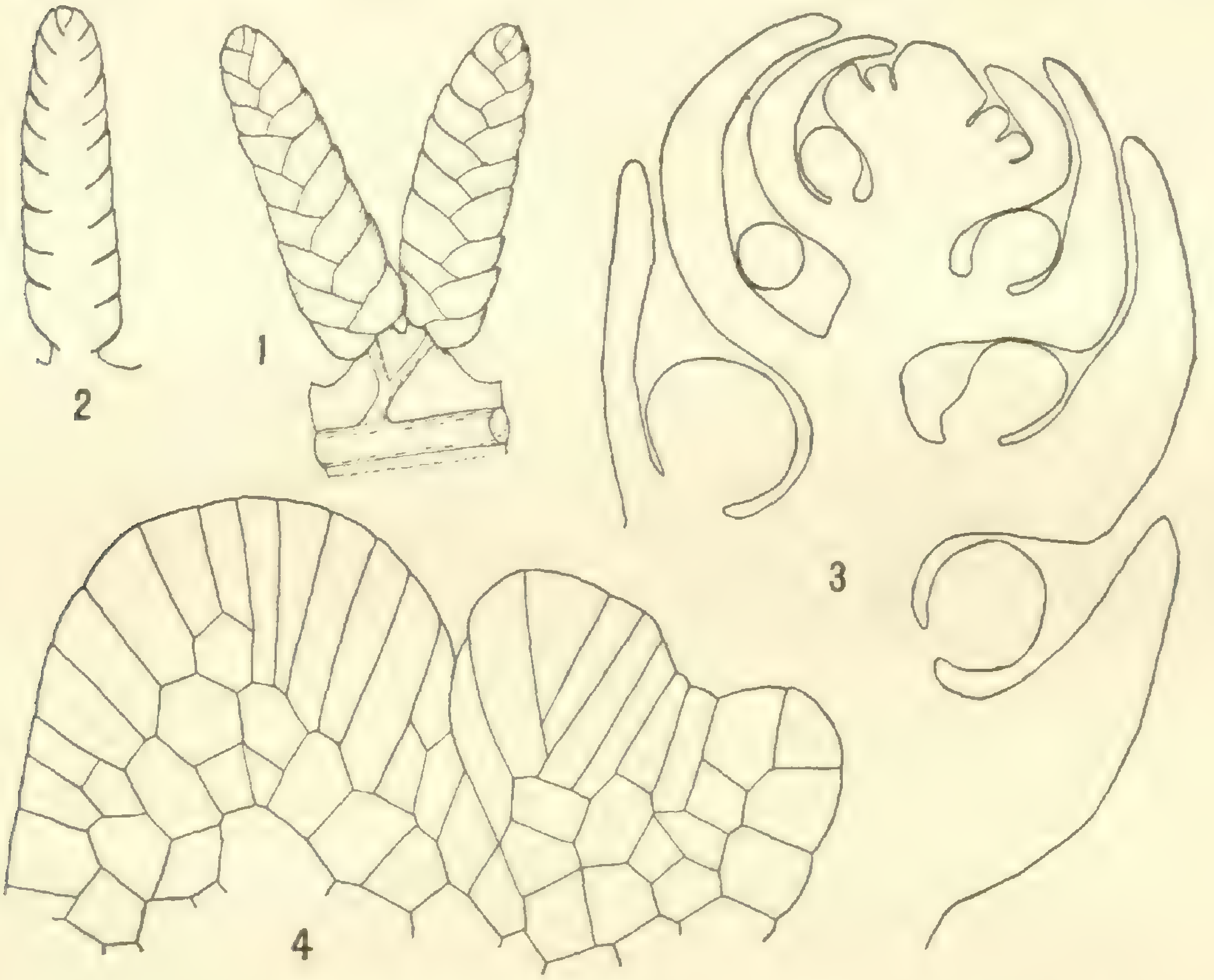

FIG. 1. Two pinnules bearing sporangia (ventral surface). ×13.—FIG. 2. Dorsal surface of a pinnule. ×13.—FIG. 3. A longitudinal section of a pinnule showing the sporangia.—FIG. 4. A longitudinal section of a pinnule showing the apex and an early stage in the development of a sporangium and indusium.

shifted from a marginal to a ventral position, and finally stands at nearly a right angle to the plane of the lacinia.

As stated above, the initial cell of the sporangium appears near the apex of a fertile portion of the leaf (*figs. 7, 8, 9*). A part of one of the segments of the apical cell enlarges and an oblique wall cuts in, either from the front or back, as shown in *figs. 10* and *11*. A second wall comes in on the opposite side from the first and at its lower edge sets upon the first (*fig. 12*); the third wall is parallel with the first and sets upon the second (*figs. 13, 14*), showing a dolabrate apical cell.[2] These

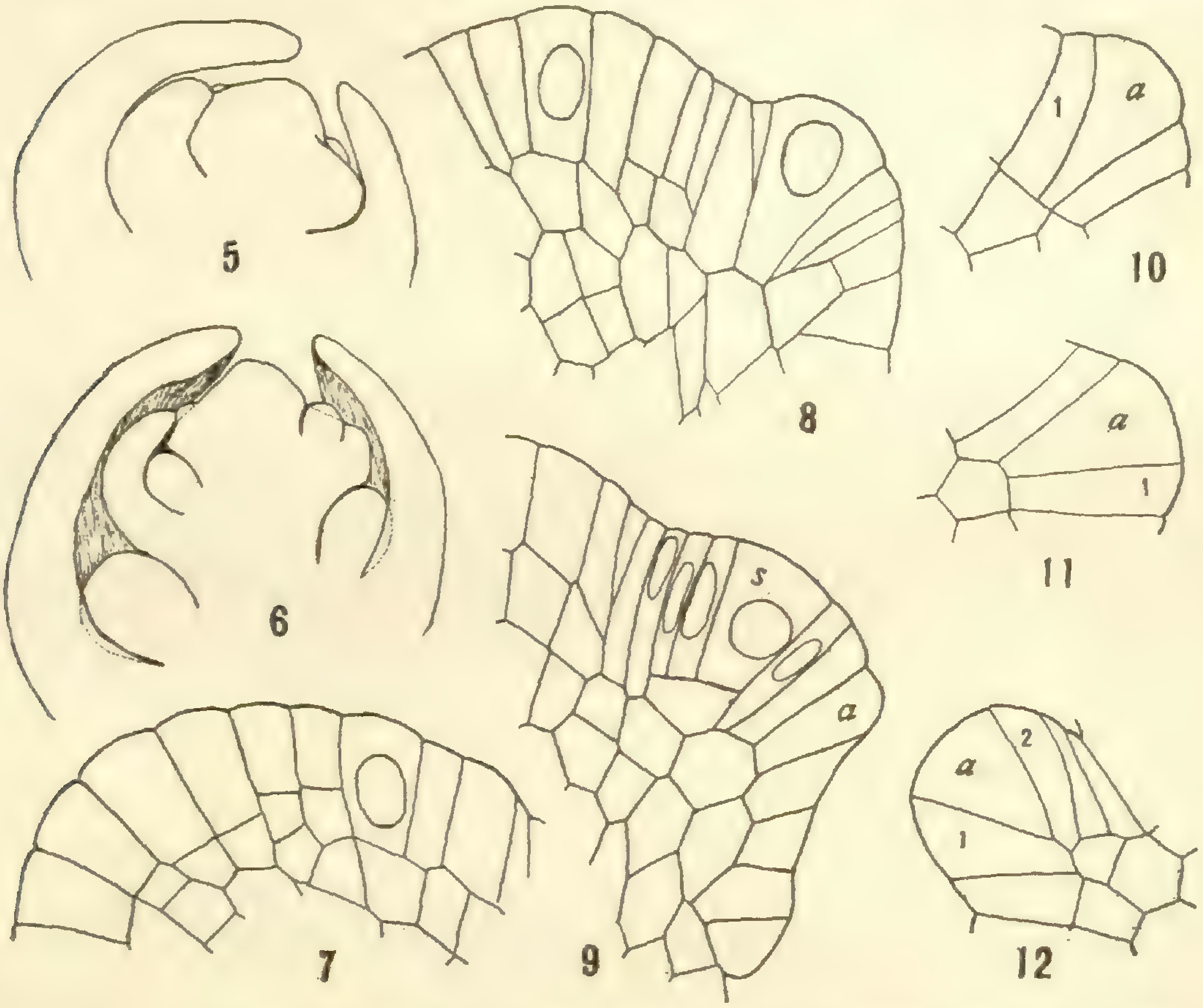

FIG. 5. The ventral side of a pinnule showing that the sporangia are soon covered by the indusium. ×130.—FIG. 6. The dorsal side of a pinnule showing the sporangia not covered by the indusium. ×190.—FIG. 7. The apex of a pinnule showing an initial sporangial cell. ×980.—FIG. 8. A longitudinal section of a pinnule showing the apical cell and a sporangial initial.—FIG. 9. An initial cell, *s*; and the beginning of the indusium, *a*.—FIG. 10. The first division of the initial cell, the first wall coming in on the anterior side. *a*, initial cell; 1, first cell cut off. ×980.—FIG. 11. The first division of the initial cell, the first wall coming in on the basal side. ×980.—FIG. 12. A section showing the first and second cells cut off from the initial cell. ×980.

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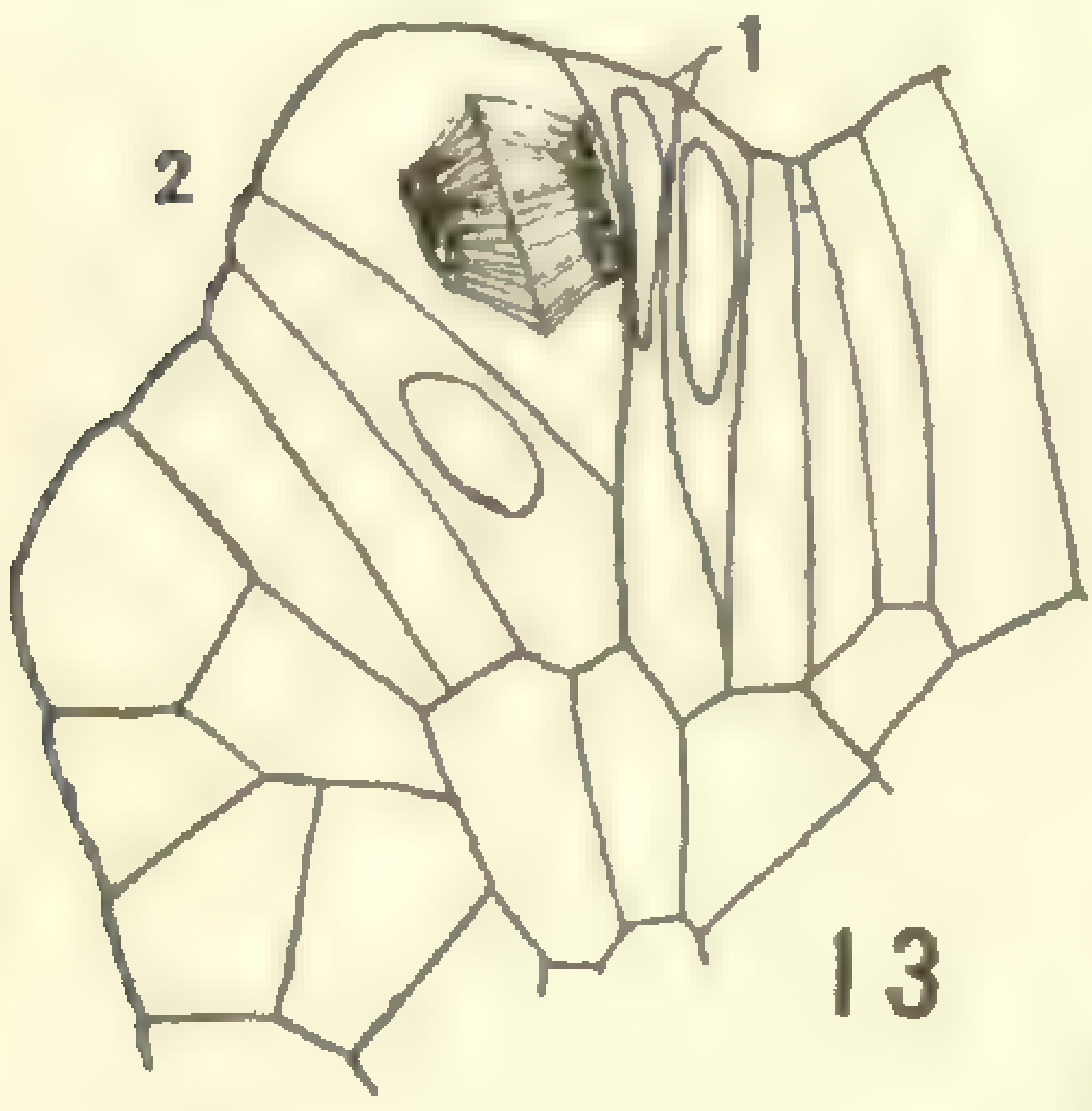
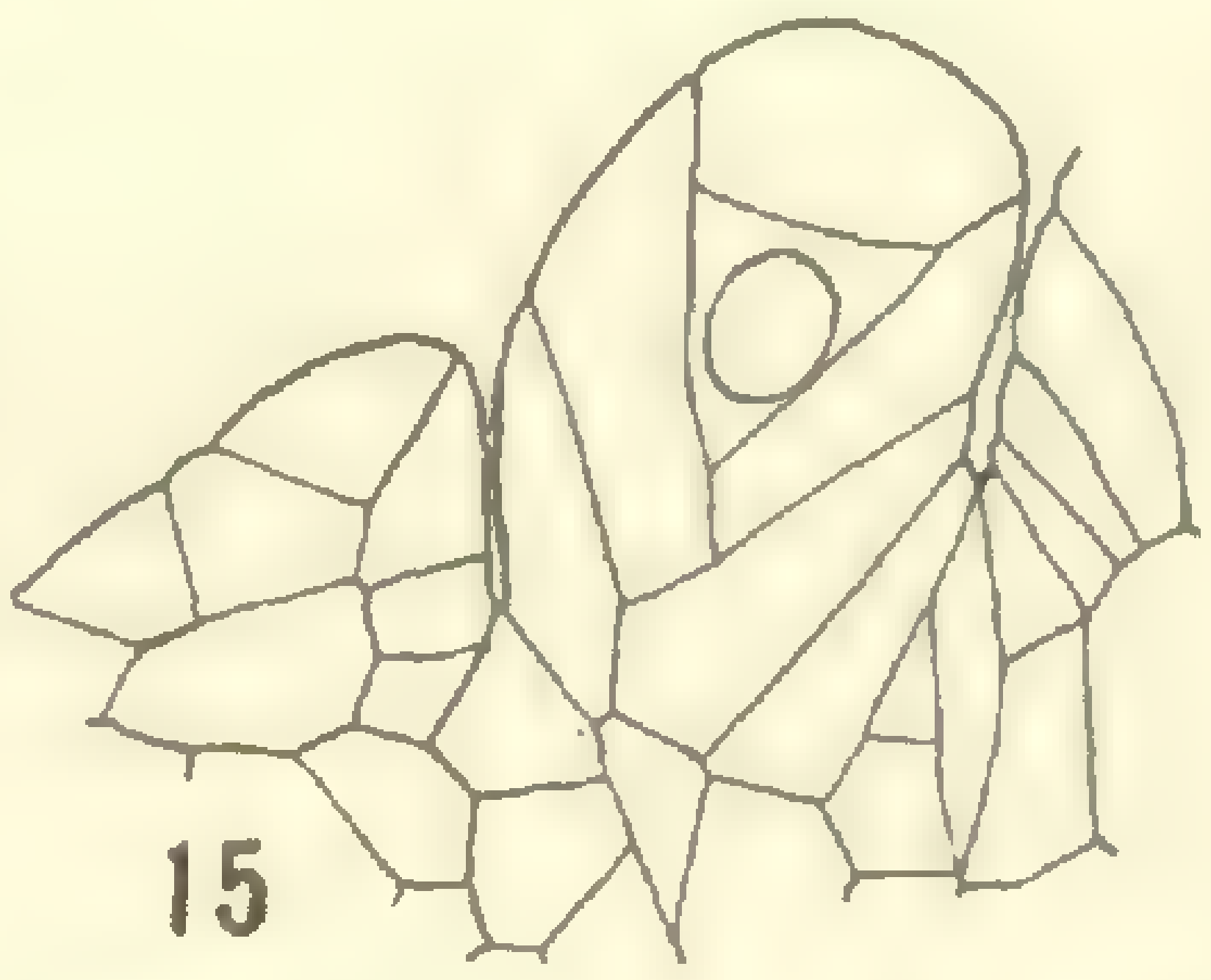
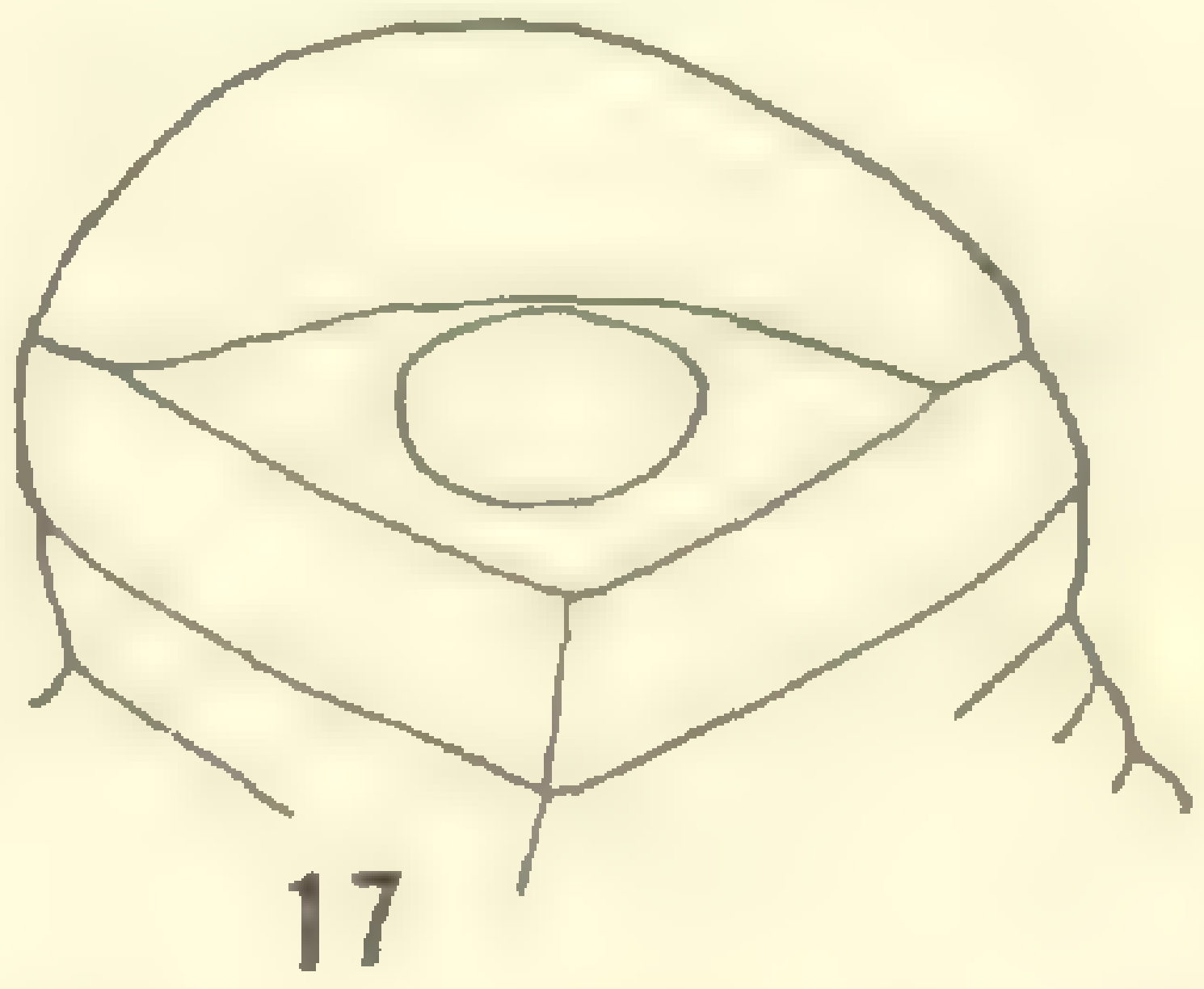
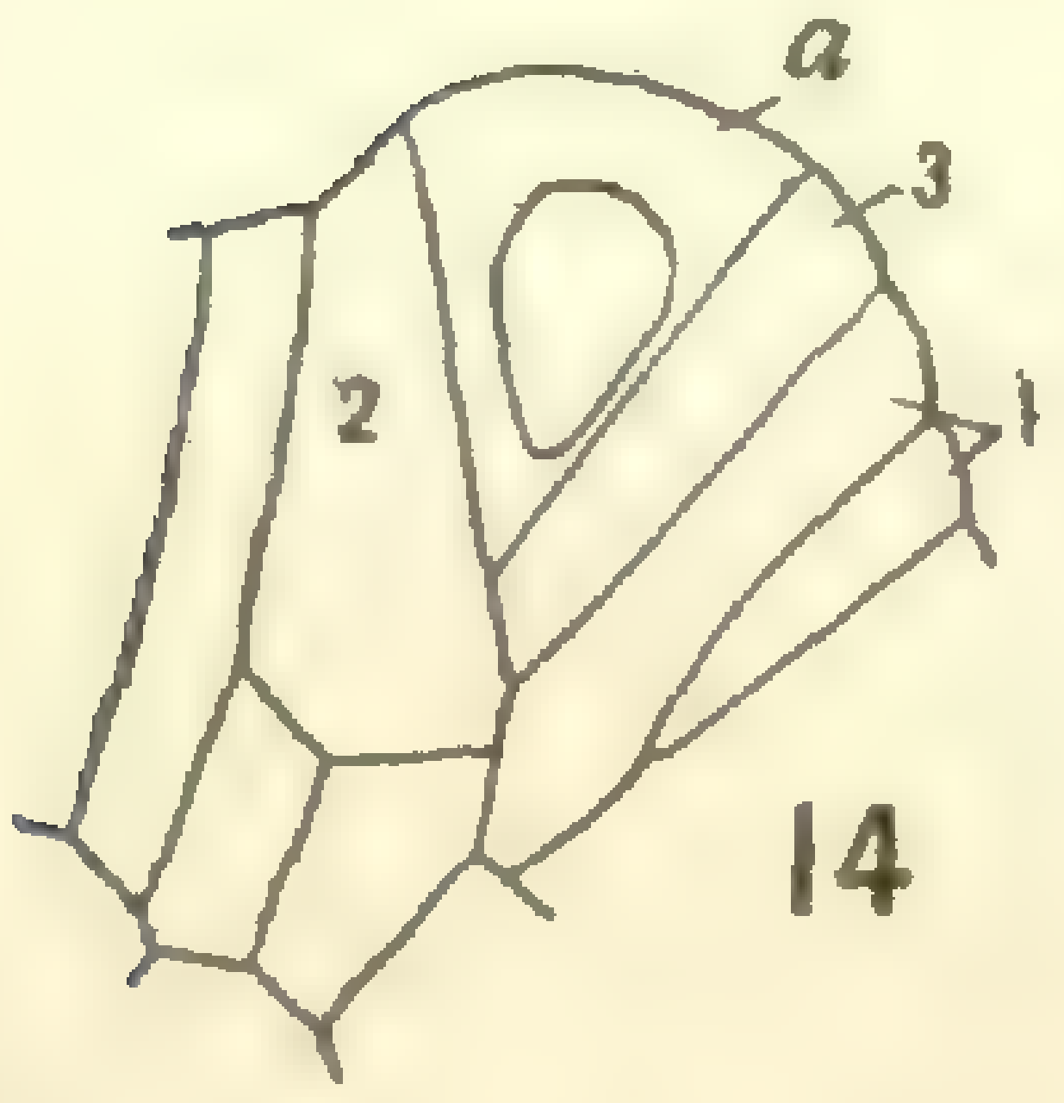
[2] I use the term proposed by Professor BARNES as an equivalent of the German *zwei-schneidige*, instead of the unfortunate translation "two-sided."

walls are usually at right angles to the plane of the leaf. These divisions, which are peculiar ones in the ontogeny of a sporangium, may be the result of the marginal initial cell. This question naturally arises: Is the position of this cell such that the conditions which determine the direction of walls cannot produce the usual tetrahedral form? I know of no other fern which has the sporangia arising on the margin of a layer of tissue one cell thick. I found one instance in which the walls were not at right angles to the lamina of the pinnule.









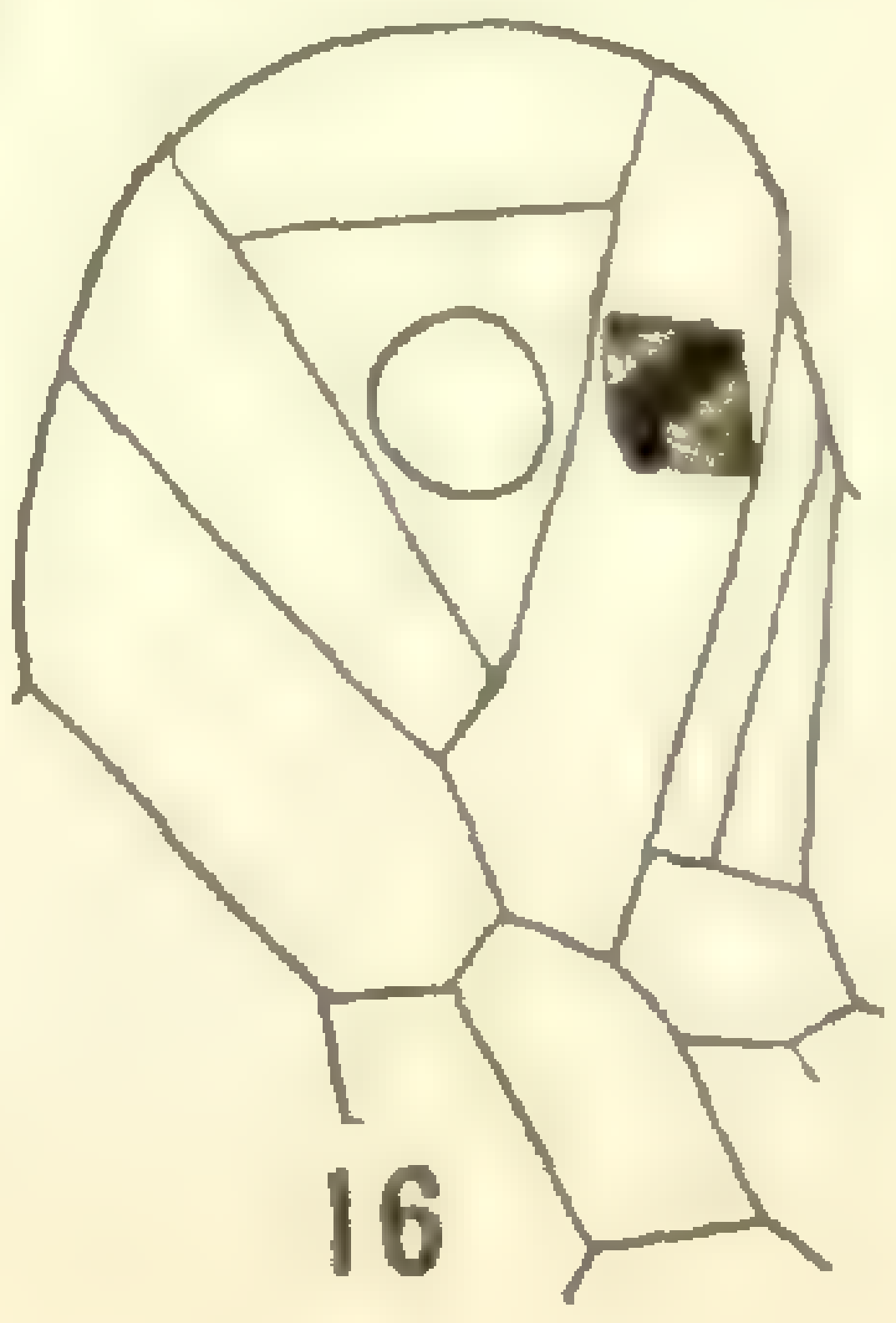
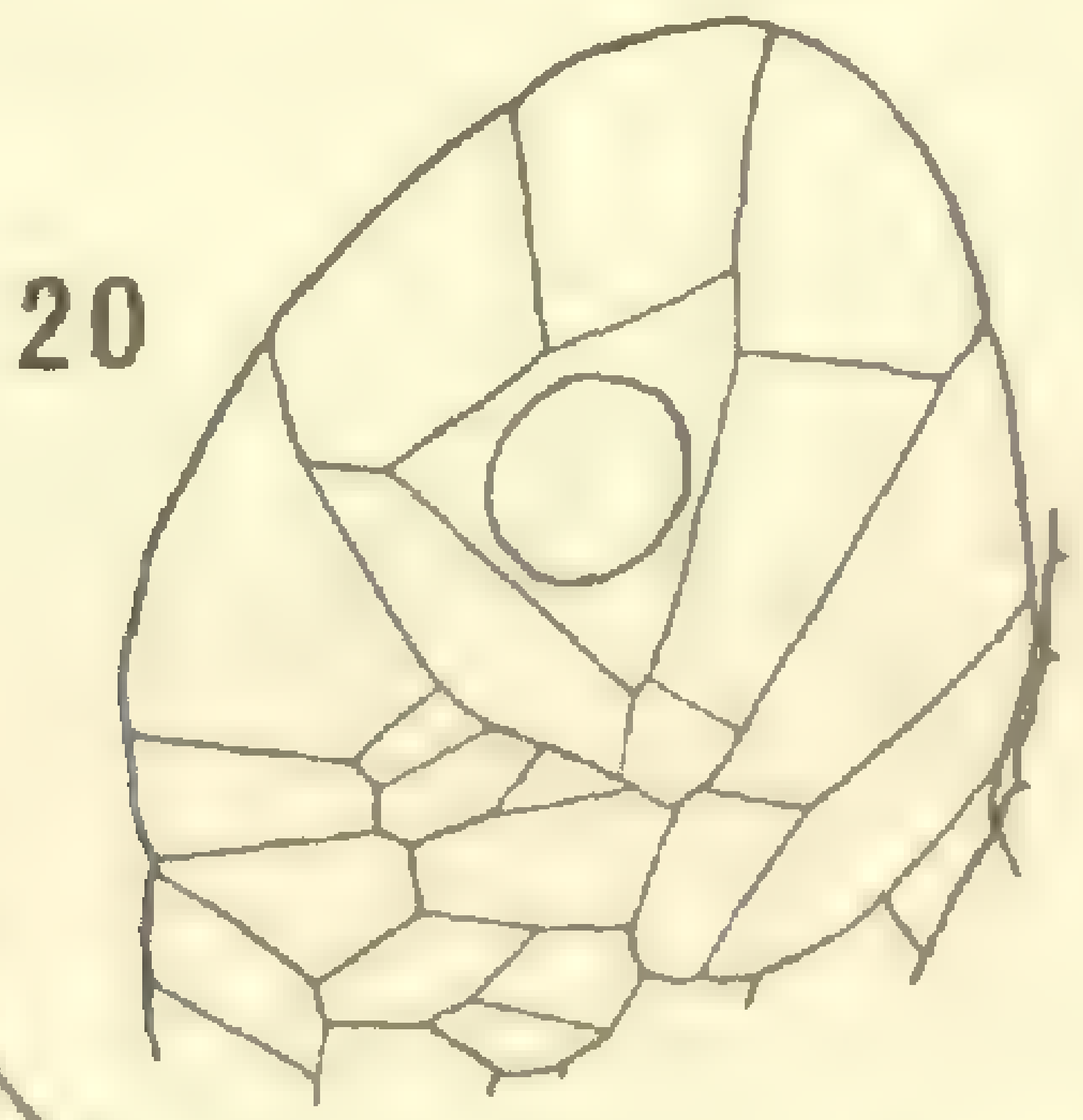
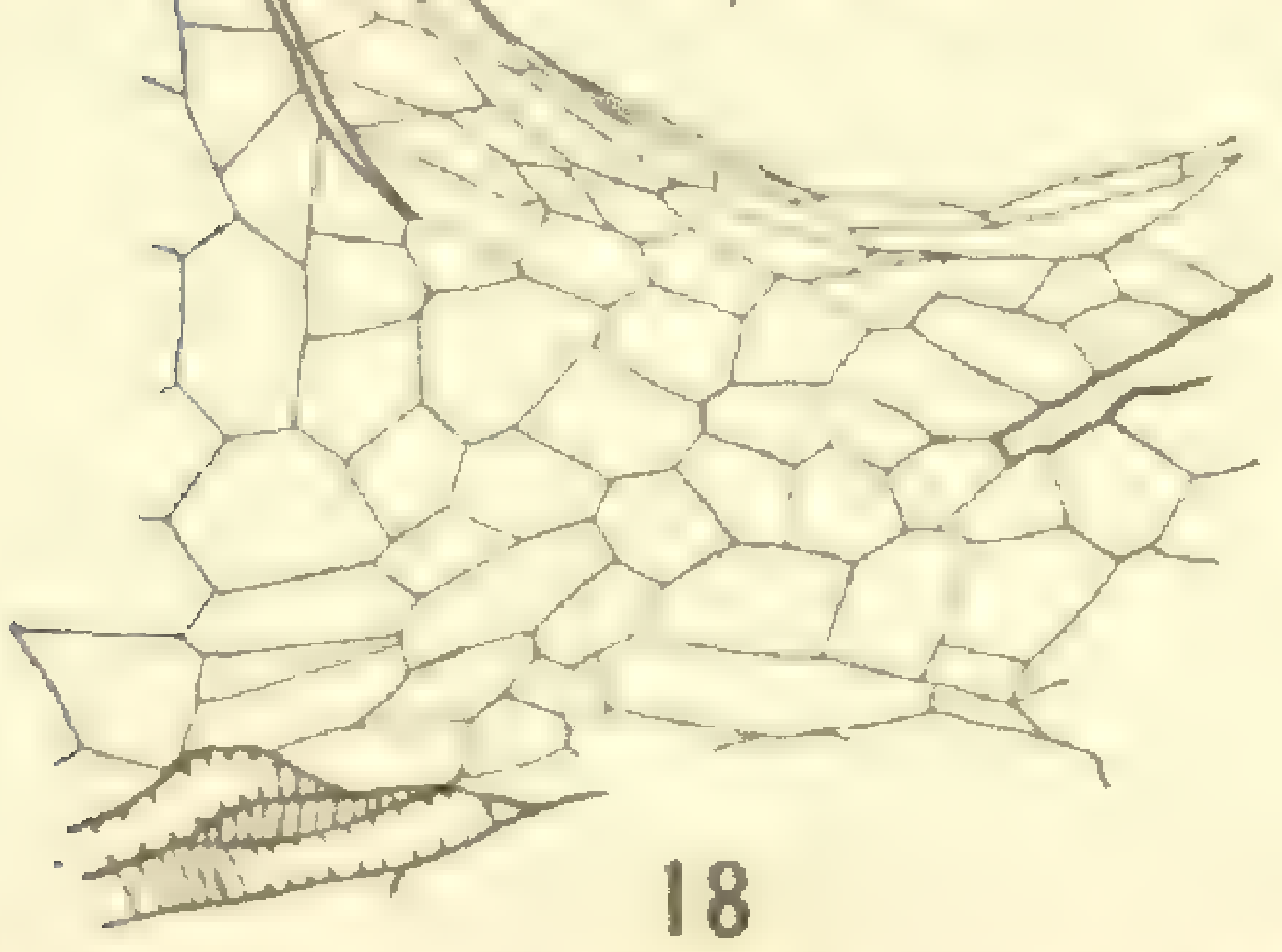


Fig. 13. The third division of the initial cell. ×980.—Fig. 14. The third division completed. ×980.—Fig. 15. A section showing the cap cell cut off by the fourth division.—Fig. 16. A section showing the cap cell and a division of a wall cell. ×980.—Fig. 17. A section perpendicular to the surface of the leaf showing the long axis of the cap cell. ×980.





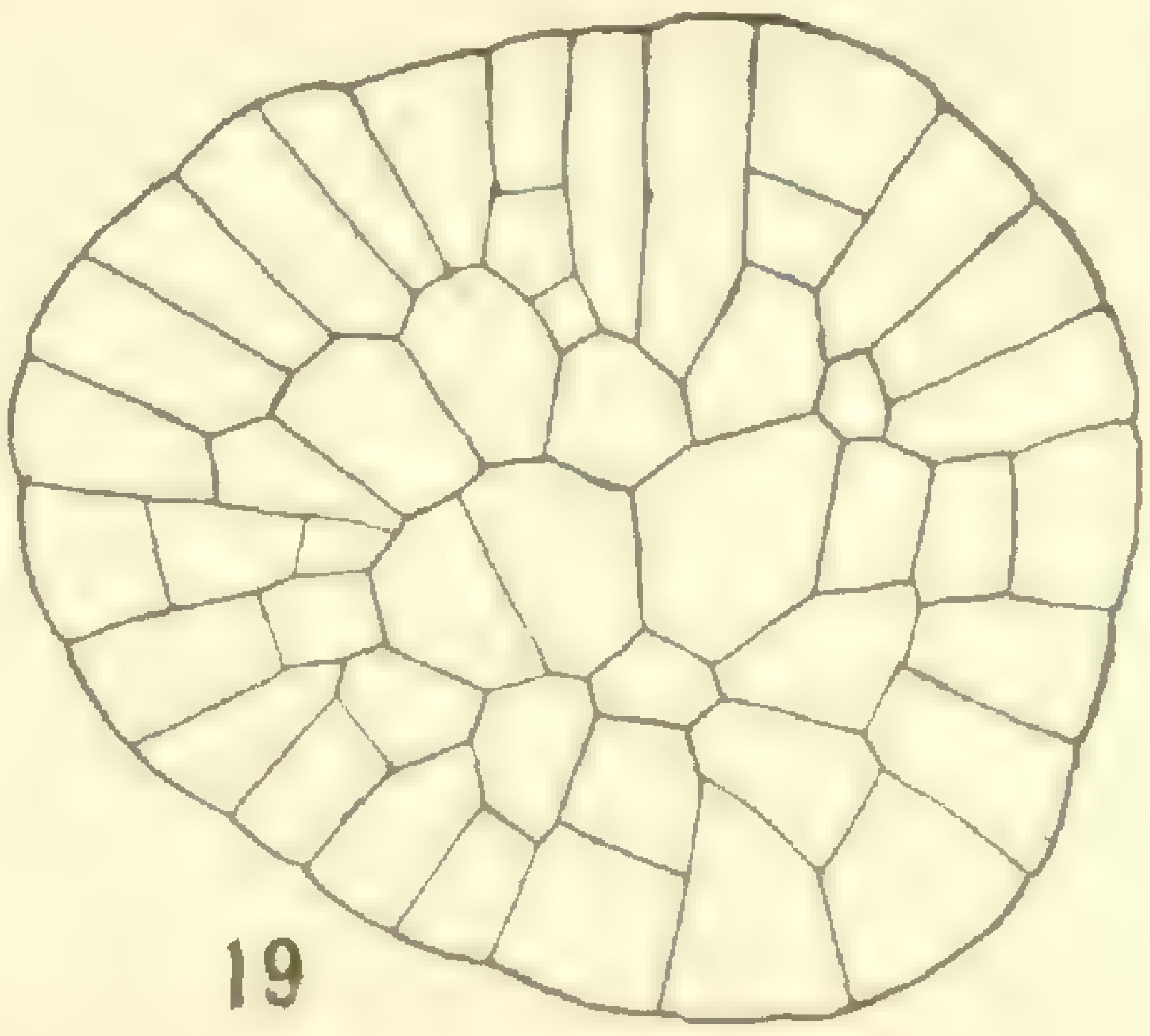


Fig. 18. A longitudinal section of the stalk of the sporangium showing the stalk to be very short.—Fig. 19. A cross-section of the stalk. ×980.—Fig. 20. A section of a sporangium showing the early division walls of the stalk and wall cells.

The fourth division cuts off the cap cell (*figs. 15, 16*), which in longitudinal section perpendicular to the leaf surface appears as an arch over the central cell (*fig. 17*). This is the longest axis of the cap cell.

THE STALK.—The stalk is short and thick (*figs. 18, 19*), the first cells cut off from the sporangium initial dividing first by anticlinal and then by periclinal walls to supply its cells (*figs. 16, 20*). *Fig. 20* shows that the adjoining cells also contribute to the stalk.

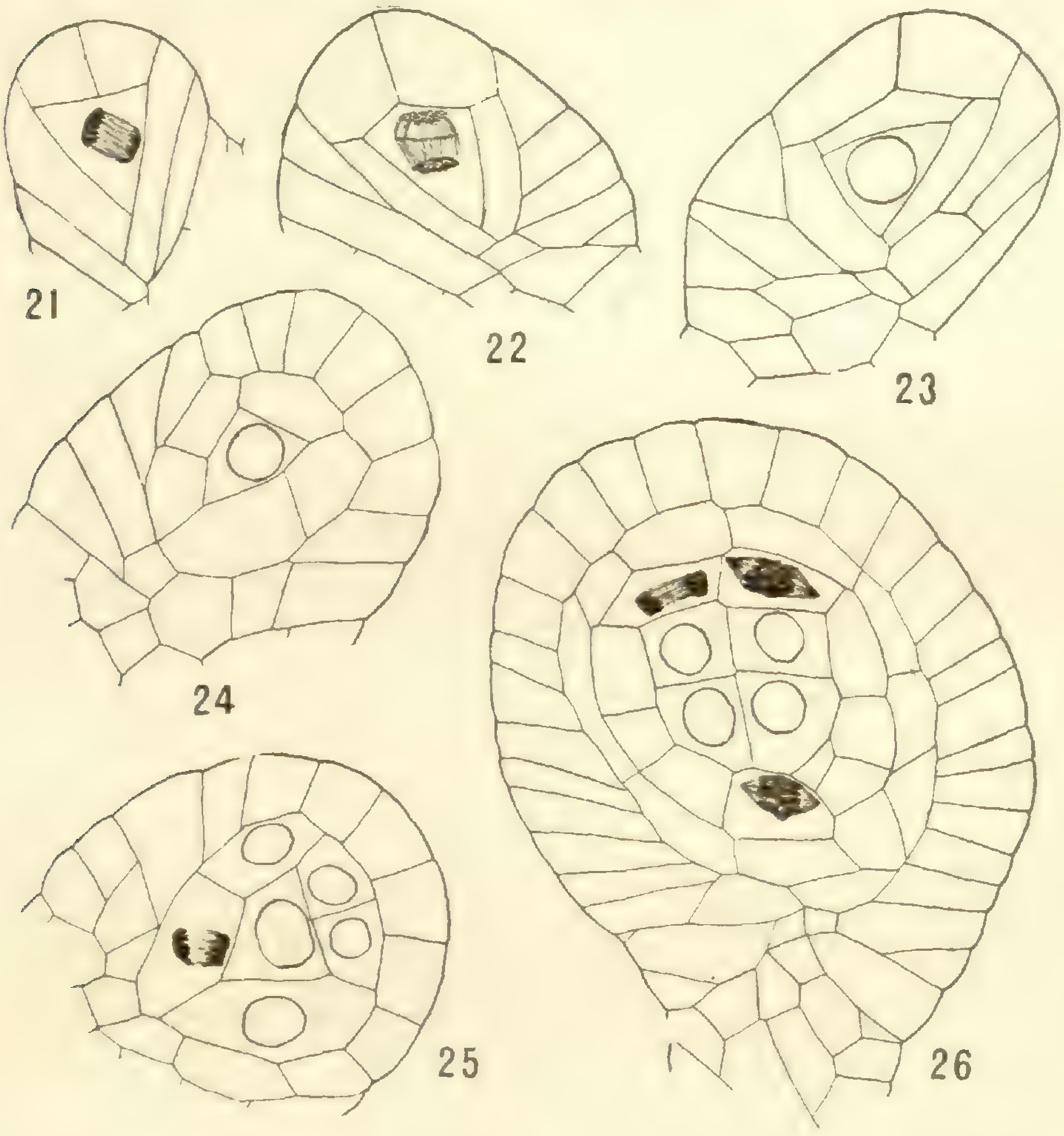
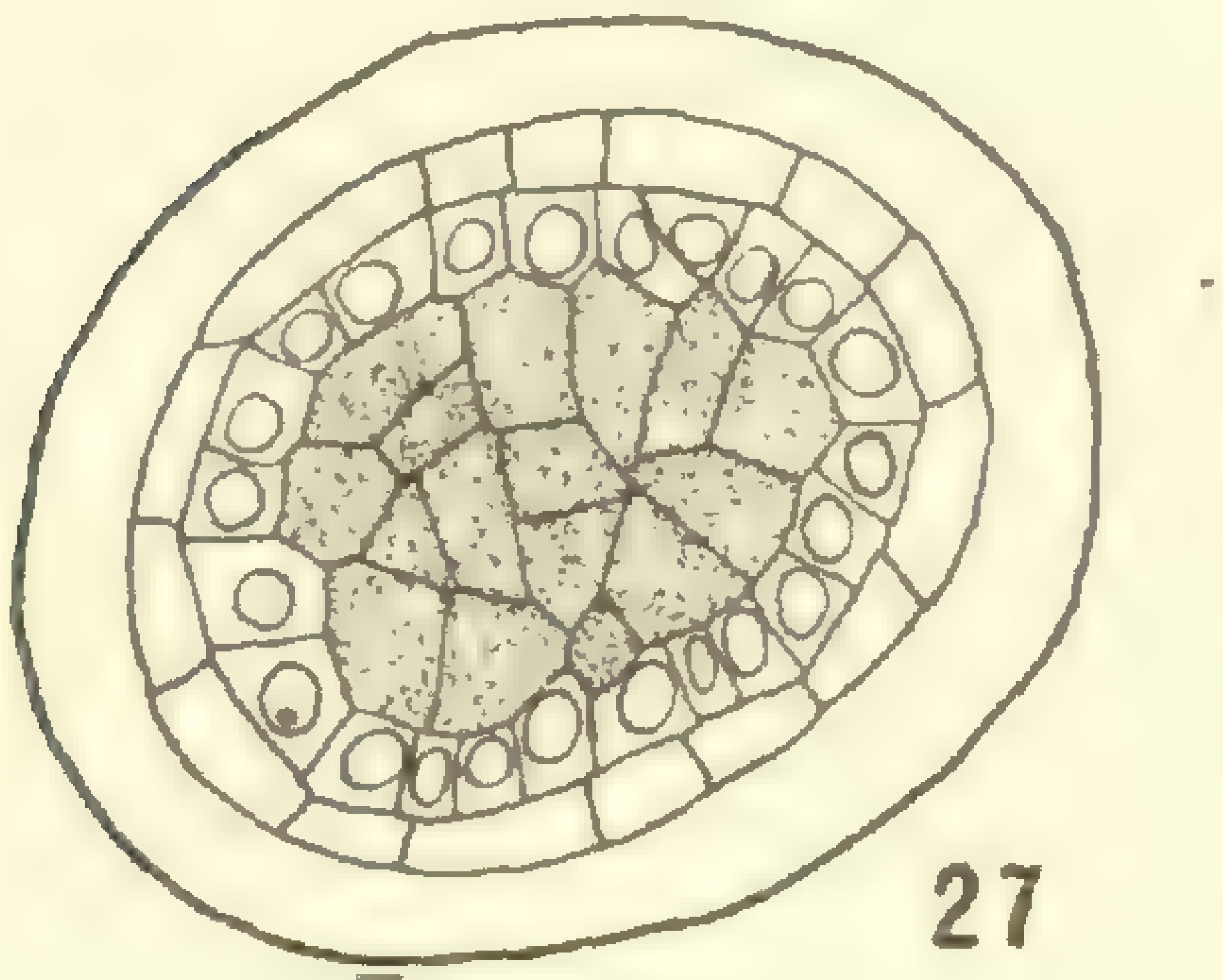


FIG. 21. The first division of the central cell. ×980.—FIG. 22. The third division of the central cell to form the third tapetal cell. ×980.—FIG. 23. The young sporangium after the three tapetal cells have been cut off.—FIG. 24. Anticlinal walls in the tapetum.—FIG. 25. The first periclinal division in the tapetum.—FIG. 26. A later stage in the development of the tapetum.

THE TAPETUM.—The tapetum is cut off from the three convex surfaces of the central cell (*figs. 21, 22, 23*); the cells divide by anticlinal (*fig.* 24) and then by periclinal walls (*figs.* 25, 26), making a many-celled tapetum of two layers (*fig.* 27). It is not always definitely two layered, as shown in *figs.* 28 and 29.

When the sporogenous tissue has reached the mother-cell stage, or somewhat before, the inner layer of tapetal cells becomes greatly enlarged (*fig.* 29), while the wall of the sporangium rapidly increases in size. Many of the cells of the tapetum become binucleate during this period and the nuclei are together in the end next to the sporogenous cells. Finally the inner layer of the tapetum is disorganized and the cytoplasm flows in around the spore mother cells (*fig.* 30).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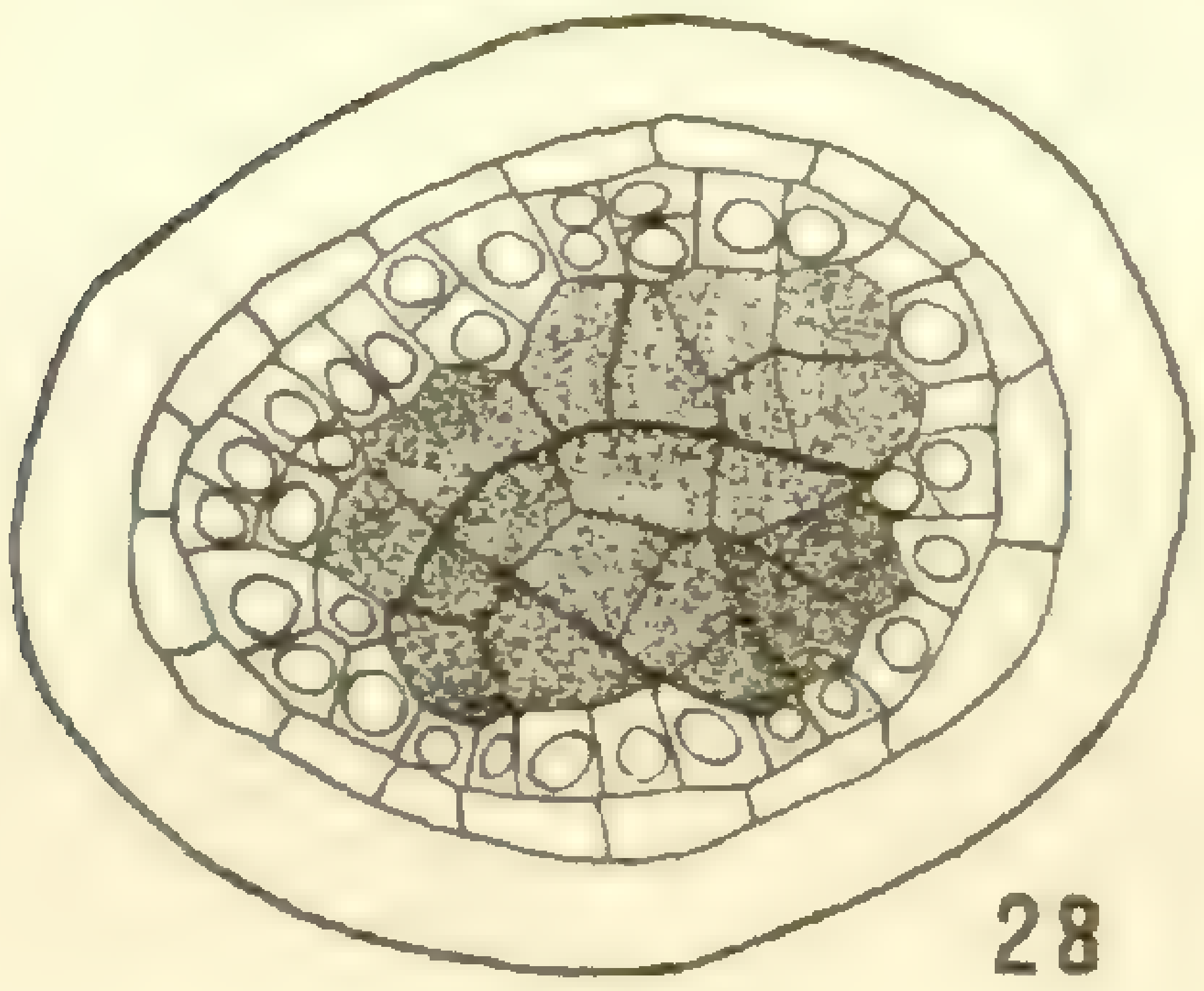
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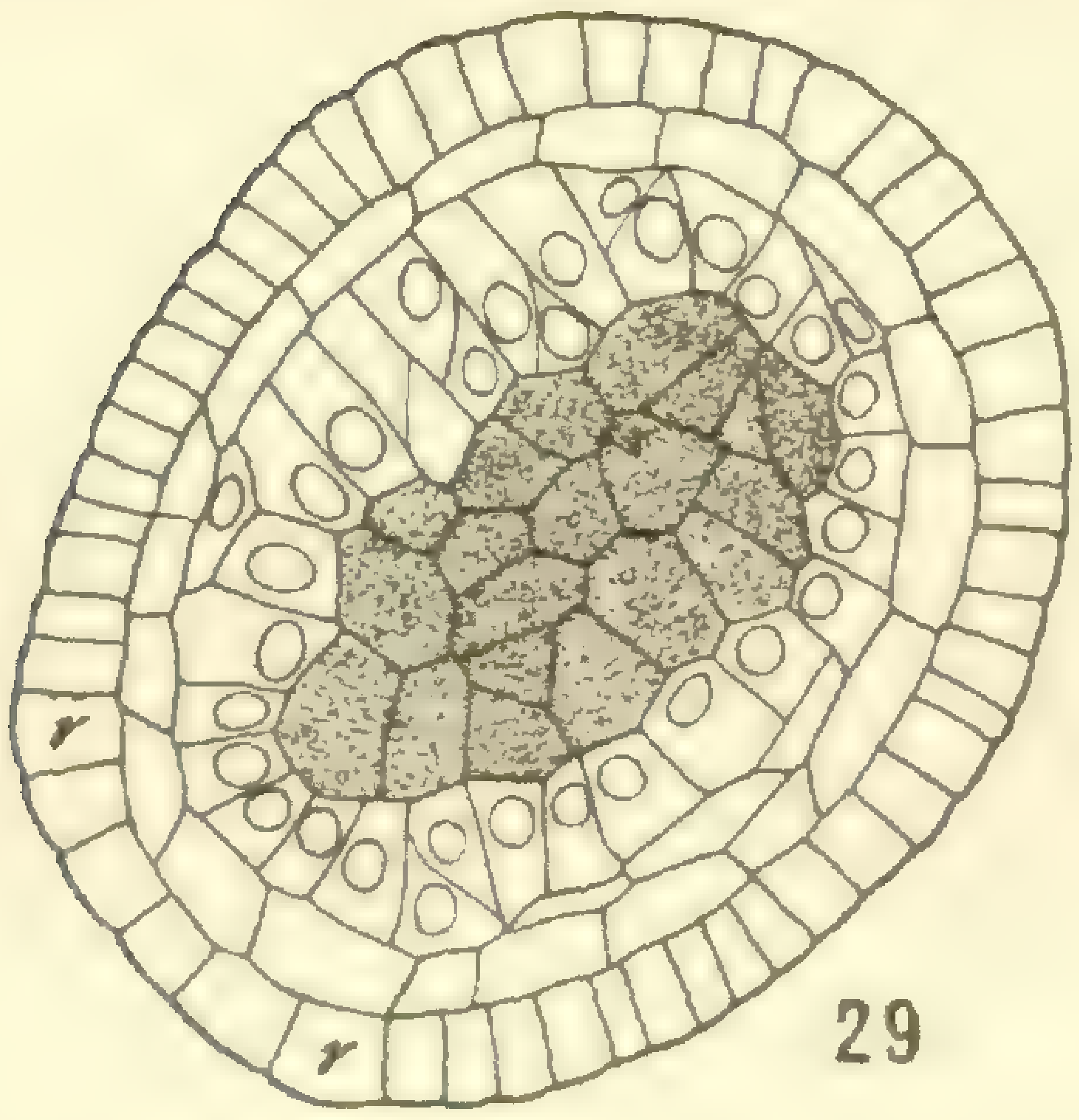

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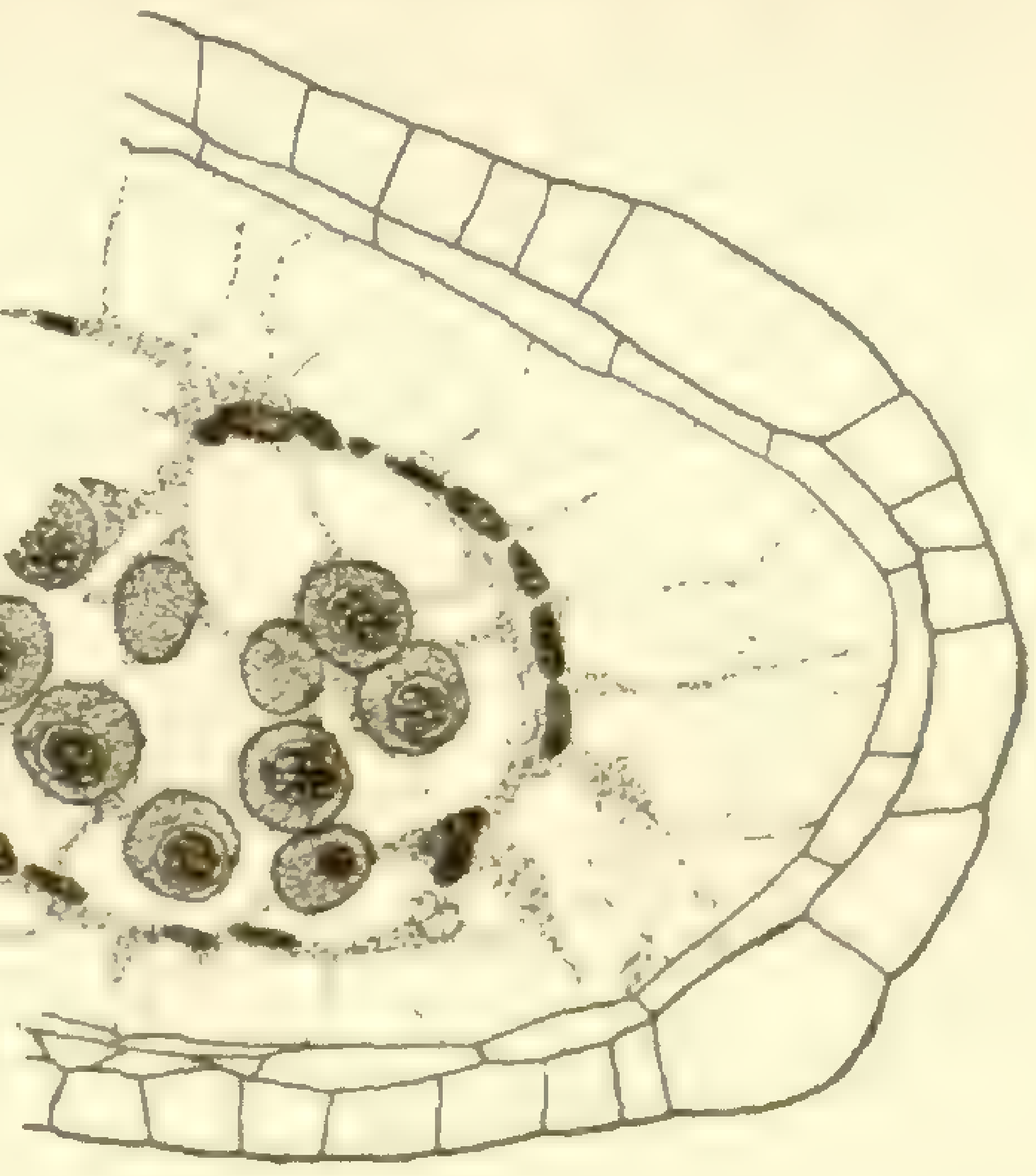
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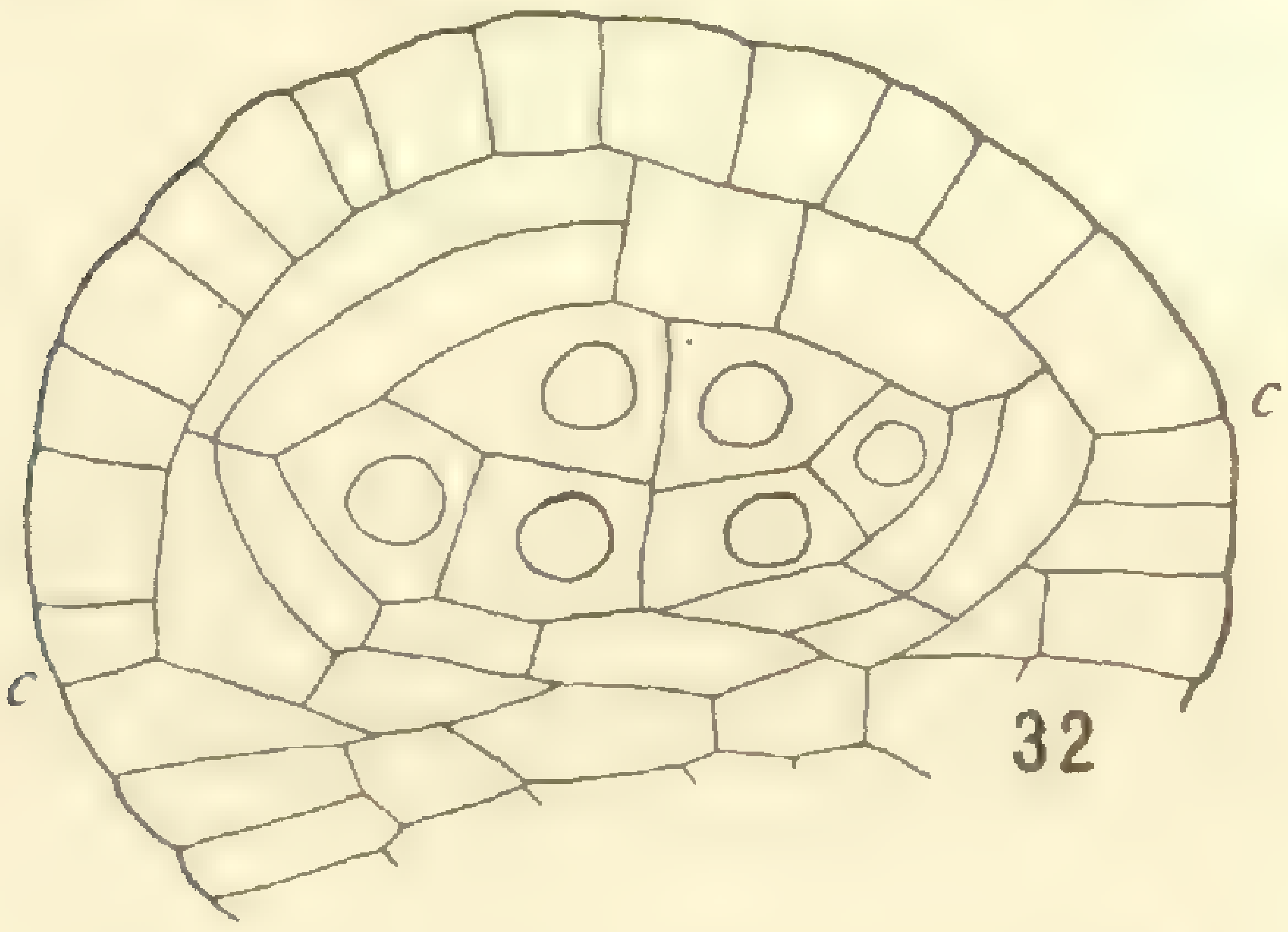
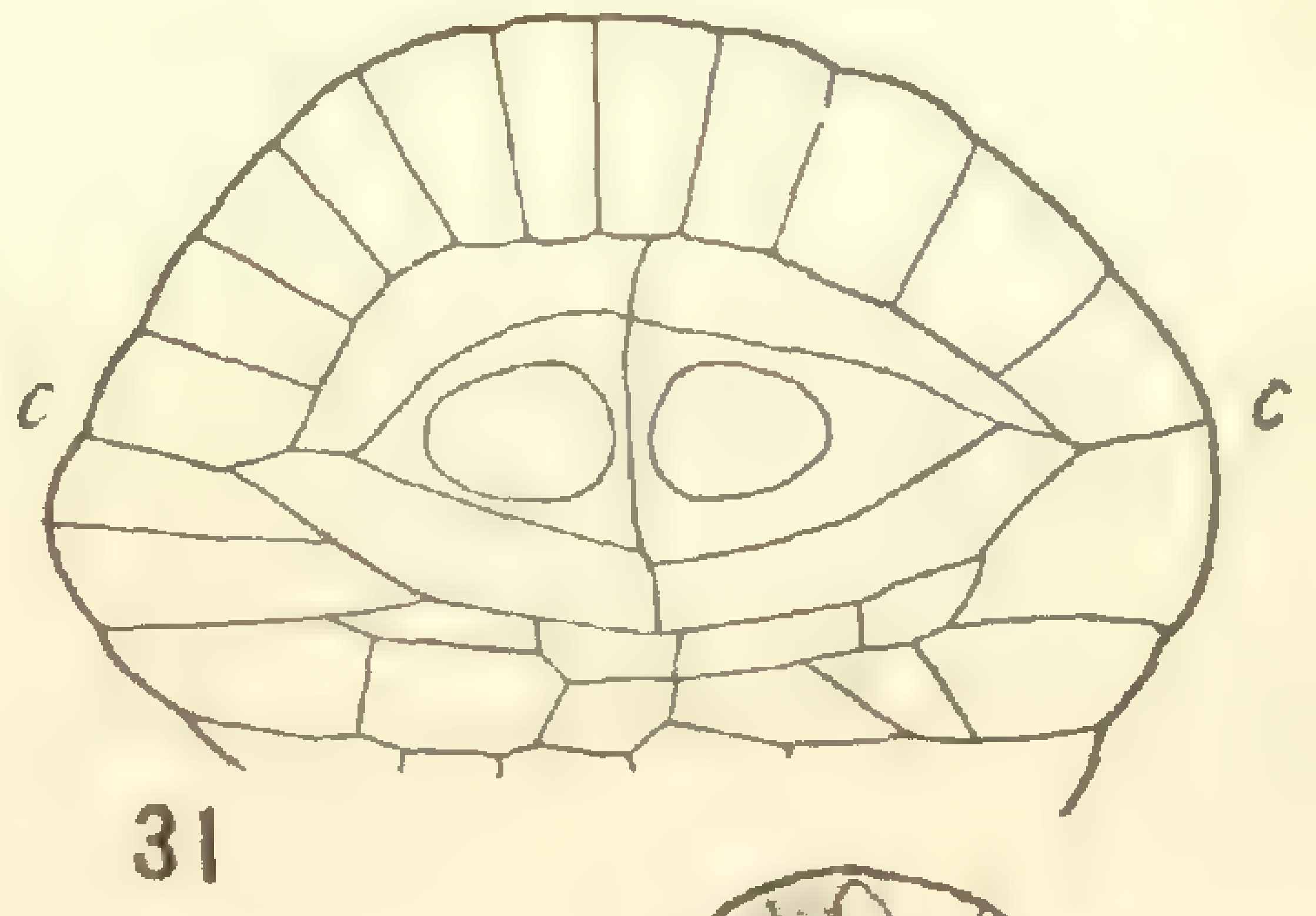
FIG. 27. A section of the sporangium showing the sporogenous mass and the two-layered tapetum. ×480.—FIG. 28. A section of the sporangium showing a doubling of the inner tapetal layer. ×480.—FIG. 29. A section showing a further development of the inner tapetal layer and the beginning of the annulus, *r*, *r*. ×480.—FIG. 30. The spore mother cell stage of the sporangium and the breaking down of the tapetum. ×480.

This development of the tapetum seems to be related to a rather large sporogenous mass where nutrition is difficult. The order of events is as follows: first a comparatively small amount of growth in the sporogenous mass up to the mother-cell stage, and then a large growth of the sporangium wall. When the spore mother cells have rounded off and the tapetum has entered in between them, conditions are good for the growth of these cells and the spores, which then grow rapidly. Thus we have an alternating growth between the sporangium wall and the spores, which relieves the nutritive strain.

The wall.—The outer wall of the sporangium is formed mostly from the cap cell (*figs. 31, 32*). The first wall formed in the cap cell is said by Prantl to be parallel with the leaf surface, but I find that its position varies. *Fig. 33* is from a section cut parallel with the leaf surface and it is here seen that the first wall is perpendicular to plane of the lamina.





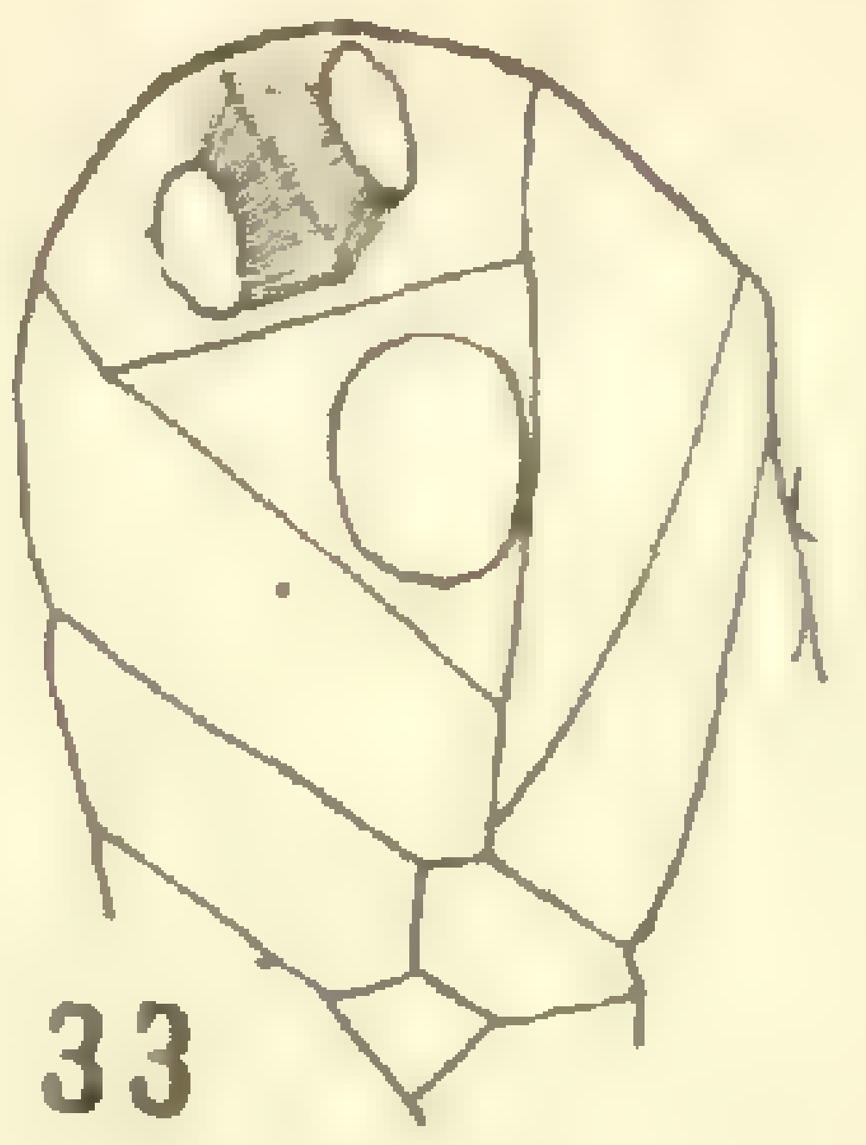


Fig. 31. A section showing the cells derived from the cap cell arched over the sporangium from *c* to *c*. ×980.—Fig. 32. A section of a sporangium somewhat older than the one shown in *fig. 31*. ×980.—Fig. 33. A section of a sporangium, cut parallel with the surface of the leaf, showing the first division of the cap cell. ×980.

The annulus appears as a circle of cells, one to three cells wide, on the costal side of the sporangium (*figs. 29, 30*). These cells become much elongated in the direction of their axes, which are parallel with the sporangium wall and with the cell walls which separate them one from the other. This development gives the sporangium a beaked appearance. The ring is widest on the upper side, where the thick-walled cells of the annulus extend out along the sides of the stomium, which is perpendicular to the annulus and in the median plane of the sporangium. On the upper side the ring is three cells wide; on the under side it is only one cell wide. In this species the length of the annulus cells varies somewhat, so that the line which is the border of the ring is rather irregular.

The number of wall cells included within the annulus at the apical end is twelve to seventeen.

THE SPOROGENOUS MASS.—The first division wall of the archesporium is usually perpendicular to the longest axis of the central cell (*fig. 31*), which is at first perpendicular to the leaf surface. Other divisions are quite irregular, but some appear curved and parallel with the first walls of the initial sporangial cell (*fig. 28*). The outline of the sporogenous mass becomes very irregular (*figs. 27, 28, 29*), and the tapetal cells thus dip down into it; this makes possible a better nourishment of the sporogenous mass.

The sporogenous mass is rather large and made up of large cells; I have counted as many as seventy-two mother cells, but sixty-four seems to be the usual number. The number of spores per sporangium is 242 to 258 by actual count. Some of the mother cells become sterilized and function as nutritive cells (*fig. 34*). The mother cells and newly formed tetrads occupy but a small portion of the cavity of the sporangium (*fig. 30*). After the spores are formed there is a great increase in their size, so that they finally fill the large sporangium. The average diameter of the spore mother cell, newly formed tetrad, and mature spore are respectively 0.025^{mm}, 0.028^{mm}, and 0.075^{mm}. Occasionally a dwarf spore is found.

STERILE SPORANGIA.—The growth of the spores is apparently a great drain upon the pinnae, so great that the young sporangia at the apex are drawn upon for nutriment, and the sporogenous mass in these sporangia is arrested in its development. They contain no cells which take the stain in the manner characteristic of sporogenous tissue; but the cytoplasm takes on a very loose fibrillar structure and there is little material in the cell that stains at all. The outer layer of the tapetum, which usually remains a thin layer of tabular cells, takes on a very great development, the cells bulging into the cavity of the sporangium like great haustoria; *figs. 35, 36*, and *37* show various stages in this development. The cells of the wall at this time become filled with food material and stain densely.

RELATIONSHIPS.—In the evolutionary line from Marattiaceae to

Polypodiaceae, suggested by Bower, there is a progress from coherent to separate sporangia; from sporangia of definite orientation to those indefinitely oriented; from imbedded to long slender-stalked sporangia; from tapetum indefinite and derived from the tissue surrounding the sporogenous mass to a definite tapetum cut off from the central cell; from no annulus to annulus apical, oblique, and finally vertical; and from indefinite massive sporogenous tissue, not all fertile, but producing many spores, to a small definite sporogenous mass all fertile and producing few spores. In all of these particulars Lygodium falls short of the highest polypod type; in all of them also it is above the highest marattiaceous type.

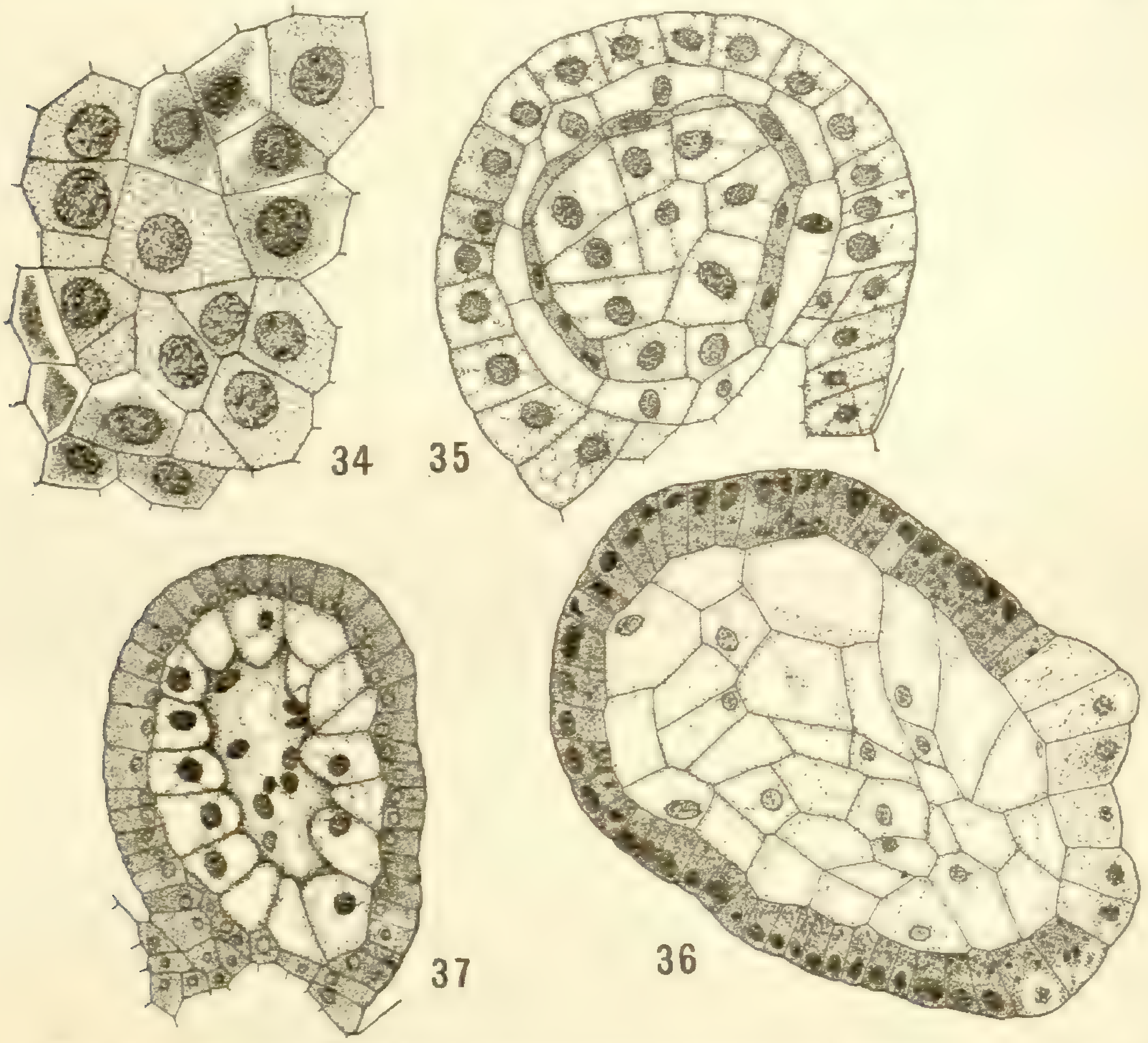


Fig. 34. A section through the sporogenous mass showing some of the cells breaking down. ×980.—Fig. 35. A sporangium near the apex of the pinnule; the sporangium is beginning to break down and will not produce spores. ×980.—Fig. 36. Another stage in the degeneration of a sporangium near the apex of a pinnule. ×480.—Fig. 37. Still another stage in the degeneration of a sporangium near the apex of a pinnule. ×480

The orientation of the sporangia is definite; this is a characteristic of the lower members of the series. The stalk is shorter and more massive than any other form above Kaulfussia. The tapetum is derived from the central cell, as in all the leptosporangiate forms; but the peculiar enlargement of the cells of the inner layer is more characteristic of the lower members of the group. The position of the annulus is the one postulated for the lower leptosporangiate ferns. The large irregular sporogenous mass in which there are occasionally sterile cells, and the large number of spores are also characteristic of the lower leptosporangiate ferns.

The family to which Lygodium belongs has some characteristics which cannot be considered as intermediate in this line of evolution, but belong to this family only. The marginal initial cell of the sporangium, whose early divisions are of the dolabrate type, is not reported for any other ferns. The single sporangium in each sorus, the large sporangium and spores, and the indusium, which in cross-section shows the tissue regions of the foliage leaf, are characteristics which in nature or degree of development belong only to this special group of ferns.

In connection with the monangial sorus, BOWER[3] has called attention to the fact that often Gleichenia has only one sporangium in a sorus near the apex of the sporophyll. A comparison made by ZEILLER[4] and emphasized by BOWER (*loc. cit.*, p. 43) brings out a close connection between the fossil form Senftenbergia and the Schizaeaceae, and also connects Senftenbergia with the Osmundaceae by means of the fossil form Kidstonia. Senftenbergia is found in lower horizons than most of the marattiaceous ferns, and is the most ancient fern whose sori are well known; these sori are monangial.

Osmundaceae, Kidstonia, Senftenbergia, and Schizaeaceae form a series in the development of the annulus, and, as BOWER (*loc. cit.*) has pointed out, the position of the annulus in Gleichenia corresponds in some points to that in the Schizaeaceae.

But after all these comparisons are made, the peculiarities mentioned above are so striking and apparently so well established, and the relations of Lygodium so ancient, that we can hardly consider it to be very close to the evolutionary line that leads to the Polypodiaceae. It seems rather to have appeared very early in the evolution of leptosporangiate ferns and to have progressed in a line somewhat divergent from the main line leading to the polypods.

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[3] Studies in the morphology of spore-producing members. IV. Phil. Trans. Roy. Soc. London B. **192**:33. ——.

[4] Bull. Soc. Bot. France **44**:95. ——.

This work was done under the supervision of Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN.

GUILFORD COLLEGE, N. C.

BRIEFER ARTICLES

NAMES OF NORTH AMERICAN TREES

The following changes in the names of North American trees as published in the *Silva of North America* and in the *Manual of the trees of North America* are made necessary in following the rules of botanical nomenclature adopted by the Vienna Congress of 1905.

Magnolia foetida Sarg. = M. GRANDIFLORA L.

Fremontodendron Californicum Cov. = FREMONTIA CALIFORNICA Torr. (Silva **14**:97).

Aesculus glabra var. *Buckleyi* Sarg. = AE. GLABRA var. ARGUTA Robs. (Silva **14**:97).

Rhus hirta Sudw. = R. TYPHINA L. (Silva **14**:99).

Ichthyomethia P. Br. being one of the genera excluded by the Congress without regard to its priority, *I. pisifera* A. S. Hitch. = PISCIDIA PISCIPULA Sarg. (Garden and Forest **4**:436).

Prunus integrifolia Sarg. (Man. 531) must be retained if this tree is considered specifically distinct from *P. ilicifolia* Walp.; but if it is considered a variety of that species it becomes var. OCCIDENTALIS Brandegee, and the variety *integrifolia* Sudw. disappears except as a synonym.

Pyrus rivularis Doug. ex Hook. = MALUS FUSCA (Rafin.) C. K. Schn.

Amelanchier Canadensis var. *spicata* Sarg. = A. CANADENSIS var. ROTUNDIFOLIA Torr. and Gray. *A. obovata* Ashe (Man. 61) = A. INTERMEDIA Spach.

Chytraculia P. Br. being one of the excluded genera, *C. Chytraculia* Sarg. (Man. 629) = CALYPTRANTHES CHYTRACULIA Sw., as published in the *Silva* (**5**:36).

Icacorea Aubl. being one of the excluded genera, *I. paniculata* Sudw. = ARDISIA PICKERINGIA Nutt.

Morodendron Britt. = HALESIA L.; *M. Carolinum* Britt. = H. CAROLINA L.; and *M. dipterum* Britt. = H. DIPTERA Ell.

Catalpa Catalpa Karst. = C. BIGNONIOIDES Walt.; *C. speciosa* Engelm. must be written C. SPECIOSA Warder ex Engelm.

Sassafras Sassafras Karst. = S. VARIIFOLIUM (Salisb.) Otto Kuntze.

Ulmus Thomasi Sarg. (Silva **14**:102) = U. RACEMOSA Thomas.

Toxylon Raf. being one of the excluded genera, *T. pomiferum* Raf. = MACLURA POMIFERA C. K. Schn.

Hicoria being one of the excluded genera, *H. Pecan* Britt. = CARYA PECAN C. K. Schn.; *H. Texana* Le Conte = C. TEXANA C. K. Schn.; *H. minima* Britt. = C. CORDIFOLIA C. K. Schn.; *H. myristiciformis* Britt. = C. MYRISTICIFORMIS Nutt.; *H. aquatica* Britt. = C. AQUATICA Nutt.; *H. ovata* Britt. = C. OVATA C. K. Schn.; *H. Carolinae-septentrionalis* Ashe = C. CAROLINAE-SEPTENTRIONALIS C. K. Schn.; *H. laciniosa* Sarg. = C. LACINIOSA C. K. Schn.; *H. alba* Britt. = C. ALBA K. Koch; *H. glabra* Britt. = C. GLABRA C. K. Schn.; *H. villosa* Ashe = C. VILLOSA C. K. Schn.

Quercus minor Sarg. = Q. STELLATA Wang.; *Q. acuminata* Sarg. = Q. MUEHLENBERGII Engelm.; *Q. platanoides* Sudw. = Q. BICOLOR Michx.; *Q. breviloba* Sarg. = Q. DURANDII Buckl.; *Q. Californica* Cooper = Q. KELLOGGII Newb.; *Q. digitata* Sudw. = Q. CUNEATA Wang.; *Q. nana* Sarg. = Q. ILICIFOLIA Wang.; *Q. brevifolia* Sarg. = Q. CINEREA Michx.

Fagus Americana Sweet = FAGUS FERRUGINEA Ait. (1789), but an older name, FAGUS GRANDIFOLIA Ehrh. (1788), should be adopted.

Alnus Oregona Nutt. = A. RUBRA Bong.

Yucca arborescens Trel. = Y. BREVIFOLIA Engelm.; *Y. radiosa* Trel. = Y. ELATA Engelm.

Tumion being one of the excluded genera, *T. taxifolium* Greene = TORREYA TAXIFOLIA Arn.; *T. Californicum* Greene = TORREYA CALIFORNICA Torr.

Sequoia Wellingtonia Seem. = SEQUOIA GIGANTEA Dec.

Pinus quadrifolia Sudw. = P. PARRYANA Engelm.; *P. attenuata* Lemmon = P. TUBERCULATA Gord.; *P. divaricata* Du Mont de Courset = P. BANKSIANA Lamb.

Larix Americana Michx. = L. LARICINA K. Koch.

Picea rubens Sarg. = P. RUBRA Dietr.; *P. Parryana* Sarg. = P. MENZIESII Engelm. (not Carr.).

Pseudotsuga mucronata Sudw. = P. TAXIFOLIA Britt.

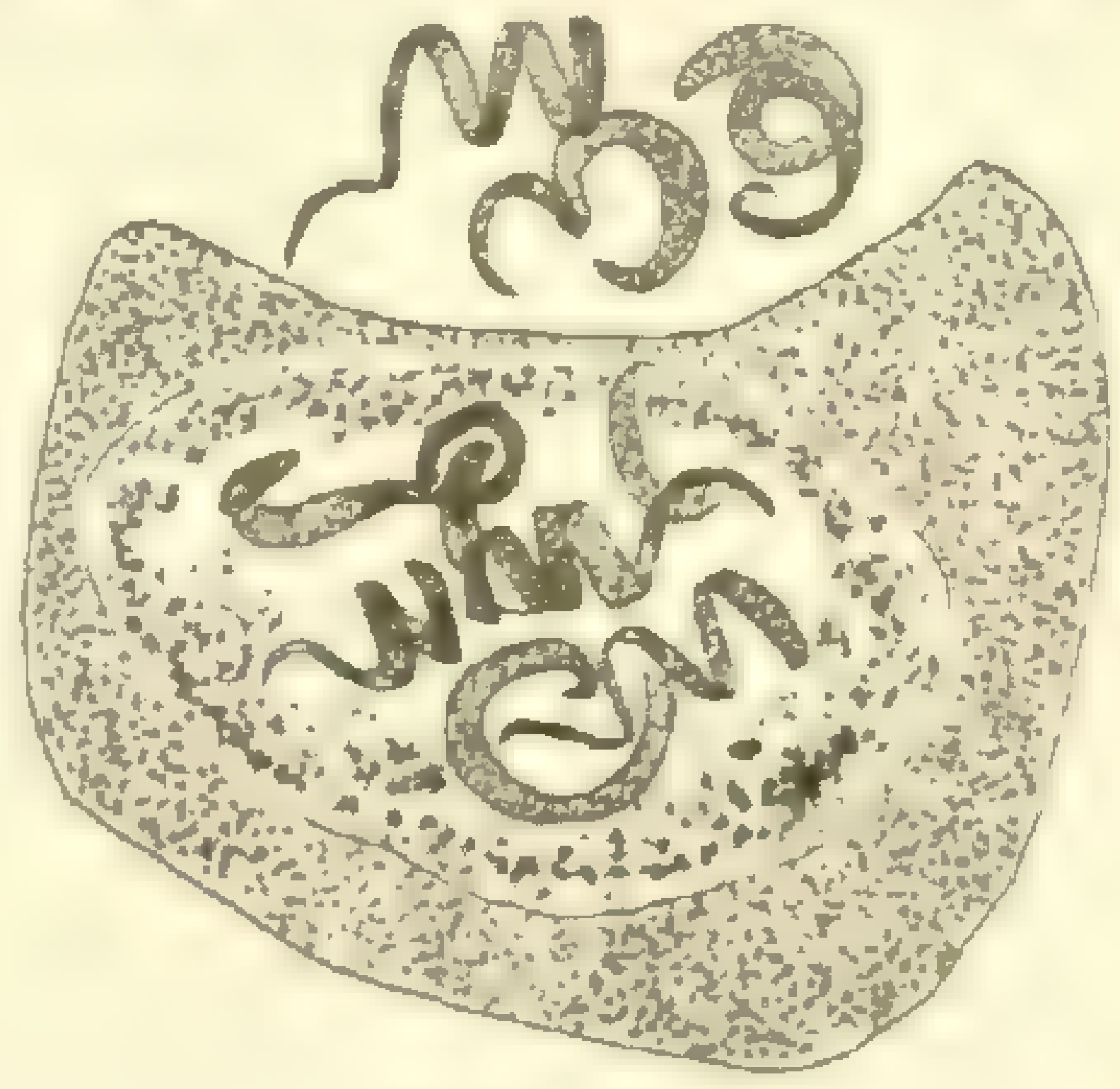
The fact that Zygia and Bucida, two of Patrick Browne's genera, have been omitted from the excluded list of genera shows how a list of this sort, prepared by a few men largely by personal preference and without regard to priority of publication, can become unsatisfactory in practice. Zygia is the oldest name for the genus usually called *Pithecolobium* Mart., and Bucida is the oldest name for the more familiar *Terminalia* L. They are in the same case as Ichthyomethia, Chytraculia, and other genera of Patrick Browne which are excluded. Moreover, the retention of Zygia is complicated by the fact that the name has been used for an African genus different from Pithecolobium, and that it is now generally recognized as the name for a section in the genus *Albizzia* Durazz.

On the whole the few changes in the names of North American trees necessitated by the adoption of the Vienna code are not greatly to be regretted. The substitution of Carya for the now generally accepted and excellent name of Hicoria for the hickories is unfortunate, although it cannot lead to much confusion. More serious is the change in the name of the Rocky Mountain spruce, now known and cultivated in all northern countries as *Picea pungens* Engelm. (*P. Parryana* Sarg. of the *Silva*). The name of this tree must now become *P. Menziesii* Engelm. (not Carr.), although this unfortunately is the name by which *P. Sitchensis* Carr. of the northwest coast, was long known, and is still cultivated in many European countries, especially in Great Britain, where it is a favorite ornamental tree.—C. S. SARGENT, *Arnold Arboretum*.

A REMARKABLE CASE OF POLYSPERMY IN FERNS

(WITH ONE FIGURE)

While studying the embryology of ferns during the past year in Indiana University, some prothallia of *Onoclea struthiopteris* were supplied me, which had been preserved ten hours after the introduction of spermatozoids. From one of these prothallia especially good preparations were obtained, showing various stages in the development of archegonia up to normal fecundation. Two cases of polyspermy also were found, of which the most remarkable one is shown in the accompanying figure. No less than seven spermatozoids were counted, entirely within the nuclear membrane and occupying the central part of the nucleus. Nothing in the appearance of the egg, either in the cytoplasm or nucleus, indicated an abnormal condition of the egg or egg nucleus. The chromatin network was broken up and irregularly massed, but it could hardly have been otherwise after the entrance of so many spermatozoids. Four of the spermatozoids, as shown in the figure, were obtained entire in one section, three others being cut in two and lying in the neighboring sections. Three spermatozoids, which did not succeed in entering the egg, lie in the concavity just above it.—WILLIAM L. WOODBURN, *Indiana University*.



Section of egg cell of *Onoclea struthiopteris*, showing seven sperms (four entire and sections of the other three) entirely within the egg nucleus and three sperms in the concavity above the egg cell.

CURRENT LITERATURE

BOOK REVIEWS

Two ecological monographs

Climatic adaptations.—Supported by a grant from the Royal Prussian Academy of Sciences in Berlin, Dr. CARL HOLTERMANN was able to spend some time at the botanical gardens in Peradeniya and Buitenzorg, where he carried on investigations upon the anatomy and physiology of tropical plants, returning to Berlin with a very rich collection of alcoholic material, only part of which has yet been investigated. The first fruits of these investigations form a bulky volume (which might easily have been made less imposing and more convenient) upon the influence of climate on the structure of plants.[1]

The work is dedicated to SCHWENDENER (in honor of the fiftieth anniversary of his doctorate), and the author naturally looks upon plants from the same view-point as the *Meister*—"dass im inneren Bau der Pflanzen eine weitgehende Zweckmässigkeit herrscht, dass Bau und Funktion bis in die kleinsten Einzelheiten in Harmonie stehen."

In the first section, on the transpiration of tropical plants, HOLTERMANN shows that both HABERLANDT and GILTAY are right in certain points. The daily maximum value of transpiration is very different in different regions; in all there are certain periods, lasting from four or five hours to one or two days, in which transpiration is so extremely vigorous that the plants suffer for lack of water. As compared with European countries, the total transpiration in 24 hours is less; in the middle of the day, however, it is often decidedly greater in the moist tropics, values being obtained which are not reached even in the hottest days in Berlin; yet these maxima usually last only a few hours. In rainy weather, for days together transpiration ceases entirely. This, as HOLTERMANN points out, is not surprising to pupils of SCHWENDENER, who for more than a generation has treated transpiration in his lectures as a necessary physical process, which indeed induces physiological consequences, but is no indispensable function. The wonderful vegetation of those regions where the rains for months at a time are continuous, or are at most only replaced by a dense fog, speaks strongly against the prevalent view of evaporation as a function; and so do HOLTERMANN'S experiments with Impatiens, which grows well in saturated air.

The second section, on tropical vegetation zones, is devoted to showing how the members of the various plant societies show like anatomical adaptations to the climate. He directs attention especially to the water-storing tissue, which he declares to be no xerophytic character (i. e., one that serves as an adaptation to a long dry period), but to have its relation to the transpiration of plants that have only to endure short dry periods. This tissue is almost confined to leaves of tropical and subtropical regions, where by the frequent rains and by the dews, which are heavy even in the dry periods, it can daily be refilled, quite independently of the roots. This refilling HOLTERMANN claims to have established experimentally; but the report is not convincing, particularly as this process is alleged to take place through the epidermis. If water can come in so, it can go out so; and the plant would be the gainer only when the period of evaporation was shorter than the period of absorption.

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[1] HOLTERMANN, CARL., Der Einfluss des Klimas auf den Bau der Pflanzengewebe. Anatomisch-physiologische Untersuchungen in den Tropen. Imp. 8vo. pp. viii+247. *figs. 7. pls. 16.* Leipzig: Wilhelm Engelmann. 1907. *M* 12.

The third section discusses the leaf fall in the tropics. This, HOLTERMANN holds, is dependent on internal conditions which become active under the influence of climatic factors. Leaves which fall off at the beginning of a dry period are not built to withstand drought; and even if the fall be delayed by favorable conditions, it is only delayed, abscission having become a hereditary peculiarity.

The formation of growth zones is the fourth topic. The author undertakes to show that the formation of zones in secondary wood is incited by climatic factors, acting upon an inherent capacity for differentiation, which, arising originally by direct adaptation, has become heritably fixed. Just how these external factors act, he thinks, will always remain a problem.

The last section, on direct adaptation, deals with water-storing tissue, gutter-pointed and emarginate leaves, dwarfing, etc., as "caused" by definite external conditions. Such new characters, called out at first by the release of latent powers, may become fixed and heritable, just as leaf fall and growth rings, or under other conditions may again disappear.

The book is full of interesting observations, which are unfortunately not easily accessible for lack of an index.—C. R. B.

Ecology of West Australia.—The series of monographs on plant geography[2] has received a notable addition in the seventh volume, dealing with the flora of southwestern Australia,[3] by Dr. DIELS. His thorough knowledge of the herbarium material from this and similar regions, and his wide acquaintance with plant distribution made him able to plan and execute in the most profitable way the journey which he undertook in 1900–1902, in company with Dr. PFITZER, with the support of the Humboldt fund of the Royal Prussian Academy of Sciences.

The systematic results have already appeared, in collaboration with PFITZER, in ENGLER'S *Botanische Jahrbücher*. In this volume we have first, by way of introduction, the outlines of plant distribution in the whole continent; then the history of botanical exploration in extratropical West Australia; the physical geography of this region; an ecological study of the vegetation of the southwest province, lying near the coast, and that of the Eremaea province, which fills the rest and extends far beyond the bounds of West Australia; and finally a discussion of the floristic regions, the elements of the flora, its relations to others, and its developmental history.

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[2] ENGLER, A., und DRUDE, O., Die Vegetation der Erde. Sammlung pflanzengeographische Monographien. Leipzig: Wilhelm Engelmann. 1896—.

[3] DIELS, L., Die Pflanzenwelt von West Australien sudlich des Wendekreises. Imp. 8vo. pp. xii+413. *1 map, figs. 82, pls. 34.* Leipzig: Wilhelm Engelmann. 1906. *M* 36, geb. 37.50 (subs. price *M* 24, bound 25.50).

It is quite impossible to summarize this work, or to do more than direct attention to it as a thorough and careful report of the present state of knowledge regarding this bit of that great continent. For only a beginning has been made around the edges; and only a realization of the fact that in the interior there are great stretches that probably present a nearly uniform vegetation, prevents one feeling unduly the meagerness of the present knowledge, even with this great addition.

DIELS finds that in this geologically little disturbed southwestern region there has been the quiet development of a flora quite at one originally with that in the east, though the two are now widely separated by the Eremaea province, and the eastern flora has been disturbed by competition with other elements. In the specially favorable conditions of the southwest, however, development along lines of progressive endemism has brought many genera to remarkable expansion and high differentiation. DIELS rejects as an error the idea of many authors (notably WALLACE) that the West Australian flora represents the original one, which spread east; he considers it rather as an old panaustralian one, further specialized. The Eremaea flora prevails in a climate which could not have corresponded to the conditions of the old Australian flora; it is rather a selection from the primitive flora adapted to the gradual drying and enriched from the tropical north. Finally, there has come the disturbing influence of man. Even the aborigines set fire to the "bush," and the Europeans, in the seven decades of their occupation, have wrought still greater changes.

The illustrations are numerous. Part are half-tones, from photographs by PFITZER; part are detailed drawings, after the style of the *Pflanzenfamilien*, of the characteristic species. A topical index and one to plant names (not as convenient as a single one) makes the matter readily available.—C. R. B.

Plant geography

In spite of our tardiness in reviewing it, we cannot forbear calling attention to the brief discussion of certain central topics of plant geography by Count SOLMS-LAUBACH.[4] The book has grown out of lectures, given twice in the course of twelve years at the University of Strassburg, and was prepared for the press at the solicitation of friends.

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[4] SOLMS-LAUBACH, H. GRAF ZU, Die leitende Gesichtspunkt einer allgemeinen Pflanzengeographie in kurzer Darstellung. 8vo. pp. x+243. Leipzig: Arthur Felix. 1905. *M* 8.

This work was received at the close of 1905 and was sent at once to a competent reviewer, but was overlooked and recently returned at the editors' request.

The author enters a disclaimer as to any originality except in the selection of the material and its presentation. His purpose is quite other than that of GRISEBACH, DRUDE, and SCHIMPER, who have sought to present the facts of plant distribution in a comprehensive way. SOLMS-LAUBACH discusses several large topics, whose enumeration sufficiently indicates the scope of his work: species and their alteration in time; the habitat; the occupation of habitats by species; the disturbance of the equilibrium of distribution by external causes; island floras. In discussing these topics he cites illustrative examples, but omits pictures and lists of vegetation. A historical introduction and a brief recapitulation of the most general principles of geographic distribution form a suitable preface to the special topics.

Under the topic "the species" we find a discussion of the origin both of the concept and the corresponding plant groups, in which the concepts of LINNAEUS and JORDAN and the theories of LAMARCK, DARWIN, NÄGELI, and DEVRIES are set forth. The topic "habitat" includes a discussion of the relations of external factors to plant form—"adaptations" in the broadest sense. The means and methods of distribution, which make it possible for plants to occupy a habitat, are described briefly. Alterations in the habitat by invasion of plants, and especially secular alterations of climate, such as that involved in the last glacial period, with the consequent migrations, are discussed at some length. The insular floras, as conditioned by the hindrances to plant distribution, are characterized briefly.

As a book for reading in connection with the more systematic works, these lectures will be found serviceable as well as interesting.—C. R. B.

MINOR NOTICES

Contributions from the Gray Herbarium.—The current number of this series[5] contains four parts: I. "New species of Senecio and Schoenocaulon from Mexico," by J. M. GREENMAN, 3 new species of the former genus and 2 of the latter being described. II. "New or otherwise noteworthy spermatophytes, chiefly from Mexico," by B. L. ROBINSON, new species being described under Tigridia, Schoepfia, Mimosa, Pedilanthus, Bonplandia, Brittonastrum (3), Russelia, Stemodia, Piqueria, Stevia (2), Eupatorium (10), Brickellia, Guardiola, Zinnia, Perymenium, Coreopsis, Tridax, Pericome, Tagetes, Cacalia (3), Perezia (2); and two new genera of Compositae, *Cymophora* (Helianthieae) and *Loxothysanus* (Heleneae). III. "New plants from Guatemala and Mexico, collected chiefly by C. C. DEAM," by B. L. ROBINSON and H. H. BARTLETT, new species being described under Polypodium, Paspalum, Fuirena, Myriocarpa, Polygonum, Ruprechtia, Aeschynomene, Mimosa, Tetrapteris, Euphorbia, Acalypha, Clusia, Rinorea,

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[5] Contributions from the Gray Herbarium of Harvard University, N. S. 34. Proc. Amer. Acad. **43**:19–68. 1907.

Hybanthus, Ipomoea, Cordia, Russelia, Tetramerium, Isertia, Liabum (2). IV. "Diagnoses of new spermatophytes from Mexico," by M. L. FERNALD, new species being described under Carex, Alnus (2), Heliotropium, Salvia (9), Castilleja, Ruellia.—J. M. C.

Bicentennary of Linné.—In connection with the Linnean celebration at the University of Upsala, a series of eight publications has been issued. In general the volumes contain reprints of some of the most interesting minor papers of Linné, which thus become accessible to a far greater number of readers. For example, the "Invitation du recteur pour assister aux fêtes" is a paper of 107 pages, consisting chiefly of a reprint of Linné's "Cultur der Pflanzen." The announcements in reference to the conferring of doctor's degrees in philosophy, medicine, law, and theology are four volumes of reprints. There is also a special publication, "Linné och Vaxtodlingen," edited by Swederus. The first (pp. 341) of four volumes containing the correspondence of Linné is also included. The most elaborate member of the series is the "Linnéporträtt," prefaced by a colored portrait of Linné, and containing reproductions of numerous other portraits, busts, medals, etc., as well as a description of the 515 portraits (paintings, medals, etc.) in the collection of the University. The University of Upsala has certainly spared no labor and expense in doing honor to her illustrious professor.—J. M. C.

Genera Siphonogamarum.—The tenth fascicle of DALLA TORRE and HARMS's[6] list of the genera of seed-plants continues the general alphabetical list of names, the last entry being Macrocarpium.—J. M. C.

NOTES FOR STUDENTS

Fungi in termite nests.—PETCH gives an account of the fungi found in certain termite nests in Ceylon, which grow from the combs found in the chambers. The fungus flora of the combs in their normal state seems to be limited to few species which occur almost pure. The only form on the normal comb is a hyphomycete which was not determined, but from the descriptions seems to be like Sterigmatocystis. This fungus seems to be endemic in the nests, according to the author not being found outside them.

When the combs grow old they give rise to two forms of agarics, which, however, the author regards as one species. Both have been described under several names from material sent to Europe. These agarics arise from combs at a considerable depth below the surface, so that their rootlike stalks attain an average length of 30^{cm}. The lower part of the stalk is black, while the upper portion is white. The first form is marked by the absence of an annulus and by the peculiar fact that only a single plant develops from each comb. Although a large number start, only one pushes its way to the surface of the ground. All the other rudiments fail entirely to develop, so that it is not possible to find specimens which have pushed part way through the earth. The second form differs from the first in the possession of an annulus and also in its habit. Several plants of this may arise from the one comb, while at the same time many immature specimens capable of further growth may be present in the comb. The author regards the presence or absence of the annulus as an accidental character due to the conditions of growth; and, since the forms are identical in every other respect, he considers them to belong to a single species which he calls *Volvaria eurhiza*, reducing the other names to synonyms. Whatever may be said of the identity of the two forms, this disposition is entirely erroneous, for Volvaria has a free valve at the base of the stem, but possesses no annulus. These forms, judging from the descriptions and figures, have no free valve; but one has an annulus while the other has not. They will probably find a place in Pluteus or Annularia.

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[6] DALLA TORRE, C. G. DE, and HARMS, H., Genera Siphonogamarum ad systema Englerianum conscripta. Fasc. 10. pp. 721–800. Leipzig: Wilhelm Engelmann. 1907. *M* 6.

Beside the fungi described, a third form seems to be quite universally present in the fresh termite comb, although this form, which is determined as *Xylaria nigripes*, does not appear in the nests. If, however, the combs are removed and kept under bell-jars, the Xylarias always appear, forming first a conidial stroma, which is followed by the development of perithecia. The author believes that the Xylarias do not appear in the nests merely because they are eaten off by the termites as soon as they appear. Other forms of fungi growing on the combs when placed in a moist chamber are probably accidental saprophytes.

All of the forms described are eaten by the termites. When an inhabited comb is inclosed under a bell-jar the termites eat off the heads of the hyphomycete and also the Xylaria as it develops. They also eat the stalks of the agarics, following them to the surface of the ground. It is probable, therefore, that the fungi of the termite nests form food for the inhabitants, as do the "fungus gardens" for the leaf-cutting ants. It is difficult to prove this definitely by experiment, for in the absence of other foods the termites will eat many substances which do not ordinarily form part of their ration.—H. HASSELBRING.

Sperms of Cycas.—SHIBATA and MIYAKE[7] have been experimenting with sperms of Cycas. Material was sent from southern Japan to Tokyo late in September and early in October, at which time the pollen tubes are discharging their sperms. Experiments with various solutions showed that the sperms either lack chemotactic irritability, or chemotaxis can take place only under some unknown external conditions. If chemotactic irritability has been lost, fertilization must be accomplished by mechanical means. It is interesting to note that the contents of the archegonium, while they seem to exert no influence upon Cycas sperms, nevertheless attract those of some pteridophytes.—CHARLES J. CHAMBERLAIN.

CORRENS[8] has tested the influence of external factors on the sex-condition of gynodioecious plants. His studies in the inheritance of these plants had led him to believe that some plants which he had classed as pistillate were really bisporangiate, and he now finds support for this conclusion in the fact that lessened nutrition (using the term in its widest sense) decreases the development of the stamens, and, in the cases more nearly approaching starvation, suppresses them. Gynomonoecious individuals give evidence for the same fact in that the bisporangiate flowers occupy the most advantageous places in the inflorescence, and appear in the greatest proportion at the height of the flowering season, the earlier and especially the later flowers being largely or entirely monosporangiate. The truly pistillate plants cannot be made to produce bisporangiate flowers through increased nourishment. This is held to support the author's view that the pistillate form in gynodioecious species and the staminate form in androdioecious species are fundamentally distinct and have arisen from the original bisporangiate forms by mutation, and that they are not to be accounted for as the gradual accumulations of minor advantageous fluctuations, nor as due in any way to ordinary physiological response. There is some indication of the presence of distinct "lines" in *Satureia hortensis*, in JOHANNSEN'S sense. CORRENS adheres strictly to the view that nothing heritable can originate except through mutation, holding with NÄGELI and others that the essence of mutation lies not in the size of the step but in its heritability.—G. H. SHULL.

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[7] SHIBATA, K., and MIYAKE, K., Some observations on the physiology of Cycas spermatozoids. Botanical Magazine **21**:45–48. 1907.

[8] CORRENS, C., Zur Kenntnis der Geschlechtsformen polygamer Blütenpflanzen und ihrer Beeinflussbarkeit. Jahrb. Wiss. Bot. **44**:124–173. *figs. 4.* 1907.

Halophytism.—From his study of the flora of the sea coast at Cagliari, CASU[9] found three features which appeared to depend upon the presence of marine salts in the soil: (1) the sporadic distribution of the plants and their general dwarfing; (2) the prevalence of herbaceous over woody plants in number and extension of species; (3) the prevalent ubiquity of certain species in contact with saline solutions. In order to elucidate these points, he has made a special physico-chemical study of the soil of the beach and shore at the surface and at various depths, both when seeds were just germinating and when plants were growing, and has compared the chemical composition of the plant and the soil. After summarizing the very contradictory statements made by other observers, which are due, he thinks, to the imperfect and artificial conditions used by most experimenters, he attempted to study the physiological resistance of plants to sea salts under natural conditions. His results agree in showing that the phenomena named above are quite independent of the toxic or the nutritive value of the salts and are rather a multiform effect of more general conditions. Thus, by way of summary he says: the presence of germinating plants at the time of the reactivation of vegetation depends on the presence of organic residues at the surface of the soil and on its hardness; the true factor of distribution of the species is the physico-chemical structure of the soil; the prevalence of herbs and dwarfing are due to impoverishment of the soil; neither the percentage of salts in contact with the roots nor that of any single salt has any relation to the luxuriant or to the meager development of the plants; so the problem remains unsolved why certain species live exclusively on the salt beach in contact with salts. If it is solvable, CASU says the clue must doubtless be sought in a profound and accurate study of the histological structure of the halophyte itself. To us that sounds hopeless.—C. R. B.

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[9] CASU, A., Contribuzione allo studio della flora delle saline di Cagliari. Parte III. Resistenza fisiologica della flora delle saline all' azione del sale marino. Annali di Botanica 5:273–354. 1907.

Polymorphism of Hymenomycetes.—LYMAN[10] has made culture studies of certain Hymenomycetes, giving especial attention to woody and incrusting species, the primary object of the research being to obtain further knowledge of polymorphism in the group. The summarized results contain the following facts. The basidiospores of about 75 species of Polyporaceae, Hydnaceae, and Thelephoraceae were germinated and grown in pure cultures, and about 40 per cent. of them were found to possess some secondary method of reproduction, usually mycelial oidia or chlamydospores. Oidia were not found among the Thelephoraceae and Hydnaceae, but were produced by one-half of the species of Polyporaceae studied. Chlamydospores have been known in a few agarics and in a considerable number of Polyporaceae, but, aside from certain doubtful cases, were not known among the lower Hymenomycetes. The author found them much more common, especially upon the mycelium, than was known previously, finding them in over one-fourth of the species cultivated. Conidia or other rather highly specialized secondary methods of reproduction were found in seven species, all belonging to Thelephoraceae except Lentodium. The general conclusions are that a considerable majority of Hymenomycetes possess no secondary spores; that oidia are common among the Agaricaceae and Polyporaceae, and are confined to these two families; that chlamydospores occasionally occur in connection with the basidio-fructification, and are quite widely distributed on the mycelia of all families; and that conidia and other highly specialized secondary methods of reproduction are rare, occurring more frequently in the Thelephoraceae than in the higher families.—J. M. C.

Precipitin and relationship.—The precipitin reaction discovered by KRAUS and more fully marked out by TSCHISTOWITSCH and BORDET, and others, has been used by MAGNUS and FRIEDENTHAL[11] in an attempt to show experimentally the relationship of plants. The experiments were conducted as follows. Extracts containing albuminous substances were prepared from yeast, Tuber, and Agaricus, by the method used by BÜCHNER in the preparation of zymase solutions from yeast. These extracts were injected into animals, and after 12–14 days serum from the animals was treated with small quantities of the albuminous extracts. The yeast extract gave a precipitate with the serum of the animal that had been treated with yeast extract, a slight cloudiness with the serum of Tuber, but none with the serum of Agaricus. The Tuber extract gave strong precipitation both with Tuber serum and with yeast serum, but none with mushroom serum. The mushroom extract gave a precipitate only with the serum of the animal treated with mushroom extract. From these experiments the writers infer that the yeast is more closely related to the Ascomycetes than it is to the Basidiomycetes. While the precipitin method has been used to a certain extent in attempts to show relationships among animals, too much stress should not be laid on this single experiment with plants. It is possible that albuminous substances from some plants may produce precipitins in the blood of animals that will then react with many plant albumins, just as it has been found that precipitins in animals will affect animals of more and more distant relationship depending on the intensity and duration of the treatment of the original animal.—H. HASSELBRING.

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[10] LYMAN, GEORGE RICHARD, Culture studies on polymorphism of Hymenomycetes. Proc. Boston Soc. Nat. Hist. **33**:125–209. *pls. 18–26.* 1907.

[11] MAGNUS, W., and FRIEDENTHAL, HANS, Ein experimenteller Nachweis naturlicher Verwandschaft. Ber. Deutsch. Bot. Gesells. **24**:601–607. 1907.

Sand keys of Florida.—MILLSPAUGH[12] has published the results of further exploration of the sand keys of Florida. In 1904 O. E. LANSING, Jr. was sent to examine all the islets lying to the westward of Key West, and his collections, notes, and maps form the basis of the present paper. The vegetation of each islet is mapped in a very effective way. The value of the survey is to enable future students to determine what species have come to the different islets since 1904 and what have been unable to survive; what species come first to such islets; and how species spread when brought into an untainted environment. In a summary it is shown that such species as are able to avail themselves of bird and water transportation, and can withstand or actually need a saline soil and atmosphere, are the species that lay hold of these islets. Wind transportation appears to play no part whatever in the plant colonization of these minute islets. From wide study of such areas in the Antillean region, the author concludes that the order of precedence in the vegetation-covering of the wave-formed sand keys of Florida has been as follows, the method of transportation also being indicated: (1) *Sesuvium portulacastrum* (water), (2) *Cakile fusiformis* (water), (3) *Euphorbia buxifolia* (bird), (4) *Cenchrus tribuloides* and *Cyperus brunneus* (bird), (5) *Uniola paniculata* (water), (6) *Andropogon glomeratus* (bird), (7) *Suriana maritima* and *Tournefortia gnaphalodes* (bird), (8) *Borrichia arborescens* and *Iva imbricata* (bird), and (9) *Ambrosia hispida* (water).—J. M. C.

Pythium and Chytridiaceae.—BUTLER has[13] made an extended study of the genus Pythium. The introductory part of his monograph is a somewhat lengthy account of the habits, structure, and biology of the members of the genus. The observations recorded have for the most part been described by earlier students of the group, and very little that is new is added. An observation relating to the morphology of the sporangia and conidia of the genus is of interest.

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[12] MILLSPAUGH, CHARLES F., Flora of the sand keys of Florida. Field Columbian Mus. Publ. Bot. Ser. **2**:191–245. 1907.

[13] BUTLER, E. J., An account of the genus Pythium and some Chytridiaceae. Mem. Dept. Agric. India. Bot. Series **1**[5]: pp. 160. *pls. 10.* 1907.

The writer several times divided colonies of *P. intermedium* and of *P. rostratum*, keeping one-half of each colony in running water while the other half was left undisturbed. The half-colonies in running water produced almost exclusively sporangia, while the corresponding undisturbed halves produced conidia. In the systematic part of the work, 18 species are critically described and arranged. Four of these are new, one (*P. palmivorum*) being of interest on account of its unusual habitat, growing in the terminal buds of palms which are soon killed and destroyed by the fungus. Since palms grow only by the terminal bud, its death involves the destruction of the tree. Another form (*P. Indigoferae*) is epiphytic in the waxy covering of the leaves of *Indigofera arrecta*. Under the title "Species omitted" there are added brief notes on some 18 species whose descriptions are for the most part so fragmentary that identification is impossible. In the second part, a number of species of Chytridiaceae are described, with some observations on their structure and habits.—H. HASSELBRING.

Anatomy of Uvularia and Tricyrtis.—QUEVA[14] has followed his studies on Gloriosa and Littonia by an examination of the anatomy of Uvularia and Tricyrtis, which differ from the first-named genera in having a rhizome in place of a tuberous stem. In accord with this difference, Uvularia presents a simpler structure than Gloriosa, and Tricyrtis is still simpler in the disposition of its vascular strands. The bundles in the stem of Tricyrtis are all of the same rank, while Uvularia has bundles of several ranks; the larger ones are situated near the center of the stem and form the main vascular strands of the leaves, while the smaller ones run at the periphery of the stem and run to the margin of the leaves. In place of the cambium observed in the bundles of the tuber in Gloriosa, Uvularia presents only a radial arrangement of the cells of the procambial strands. These two conditions are sharply distinguished by the author, who accordingly throws doubt on the cambial nature of the cells in the bundles of sedges and grasses, figured by PLOWMAN and by CHRYSLER. The question appears to be one of definition of terms.—M. A. CHRYSLER.

The nucleus of Spirogyra.—The excellent methods and cytological experience of the GRÉGOIRE school are well shown in a late paper by BERGHS.[15] Both the chromatic and the achromatic figures are traced in detail. The so-called nuclear network of Spirogyra takes no part in the formation of chromosomes. In the prophase the nucleolus begins to show a double nature, for the chromosomes are differentiated within it, while a second substance preserves its spherical form. This second substance divides in the plane of the future cell wall and also becomes segmented into rod-shaped pieces, after which half passes with the chromosomes to each pole to form the daughter nuclei. No spirem is formed either in the prophase or telophase. The spindle is a cytoplasmic structure; even the part within the limits of the nuclear membrane does not come from the network surrounding the nucleolus, but grows in from the outside.—CHARLES J. CHAMBERLAIN.

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[14] QUEVA, CHAS., Contributions à l'anatomie des Monocotylédonées. II. Les Uvulariées rhizomateuses. Beih. Bot. Centralbl. **22**:30–77. *figs. 49*. 1907.

[15] BERGHS, JULES, Le noyau et la cinèse chez le Spirogyra. La Cellule **23**:55–86. *pls. 1–3*. 1906.

Illinois River sand region.—In connection with the work of the Illinois Biological Station on the Illinois River at Havana, a brief survey was made of certain waste sandy areas in the neighborhood. The botanical survey was made by H. A. GLEASON,[16] whose results have now been published. The ecological factors of these peculiar areas are discussed, and four plant associations are presented. Under prairie formation the three associations are the "bunch-grass," the "blow-sand," and the "blowout;" while the single representative of the forest formation is the black-jack oak association. A list of the plants is given and the phytogeographic relationships are discussed.—J. M. C.

Sulfuric acid as a fungicide.—KRAEMER[17] in experimenting with dilute sulfuric acid as a fungicide finds that solutions from 1 part to 500 to 1 part to 1000 are not injurious to ordinary field plants such as wild cherry, elder, ailanthus, yellow dock, abutilon, and others. Roses infected with mildew were sprayed several times with a solution of one part H_2SO_4 to 1000 water without injury and with the complete destruction of the mildew. This fungicide may prove especially useful in greenhouses where mildew is often very destructive to roses and where ordinary fungicides are not applicable since they spot and discolor the foliage.—H. HASSELBRING.

Chromosomes of Oenothera.—GEERTS[18] finds 14 chromosomes in *Oenothera Lamarckiana*. In connection with a brief paper he figures several somatic divisions as well as the heterotypic mitosis in the microspore and megaspore mother cells. BEER[19] found 14 chromosomes in *O. longiflora* and GATES[20] reported 14 in *O. lata*, but 20 or more in the *O. Lamarckiana* hybrid obtained from a cross of *O. Lamarckiana* with *O. lata*. GEERTS also notes the constricted shape of the chromosomes in the anaphase and telophase of mitosis.—R. R. GATES.

Secondary thickening in Pandanus.—SCHOUTE[21] has investigated the alleged secondary growth in the stem of Pandanus, and comes to the same conclusion as

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[16] GLEASON, HENRY ALLAN, A botanical survey of the Illinois River valley sand region. Bull. Ill. State Lab. Nat. Hist. **7**:149–194. 1907.

[17] KRAEMER, HENRY, Dilute sulphuric acid as a fungicide. Proc. Amer. Phil. Soc. **45**:157–163. 1906.

[18] GEERTS, J. M., Ueber die Zahl der Chromosomen von *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. **25**:191–195. *pl. 6.* 1907.

[19] BEER, RUDOLF, On the development of the pollen grain and anther of some Onagraceae. Beih. Bot. Centralbl. **19**:286–313. *pls. 3–5.* 1905.

[20] GATES, R. R., Pollen development in hybrids of *Oenothera lata* × *O. Lamarckiana*, and its relation to mutation. BOT. GAZETTE **43**:81–115. *pls. 2–4.* 1907.

[21] SCHOUTE, J. C., Ueber die Verdickungsweise des Stammes von Pandanus. Ann. Jard. Bot. Buitenzorg II. **6**:115–137. *pls. 5–8.* 1907.

CARANO, whose paper was noticed in the March number of this journal. From a number of careful measurements of trunks of different species the author concludes that there is no secondary growth in the stem of Pandanus, and that the dimensions of the stem are to be ascribed wholly to the primary growth in the vegtative cone.—M. A. CHRYSLER.

Subsoil water and forests.—PEARSON[22] has investigated the level of forest subsoil waters in India as compared with readings made in Russia and France. The conclusions are as follows: the levels within the forest are lower and steadier than those without, the effect of rain is felt later and lasts longer within than without, and the old woods lower the level more than young woods.—J. M. C.

Mutation in Nephrolepis.—Observations upon plants of *Nephrolepis Duffii* cultivated in a warm, moist atmosphere have brought GOEBEL[23] to the conclusion that this species is a mutation from *N. cordifolia*, the mutation here being a case of atavism. He believes that this and other cases of mutation in ferns may be due to adaption to environment.—CHARLES J. CHAMBERLAIN.

Leguminosae of Porto Rico.—Miss JANET PERKINS[24] has published an account of the Leguminosae of Porto Rico, 67 genera and 141 species being recognized. One genus (Stahlia) and eight species are peculiar to the island. The number of genera is rather remarkable, the largest being Cassia with 16 species. No new species are described.—J. M. C.

Crossing of Reana and Zea.—VILMORIN[25] has reported the crossing of a species of Reana (teosinte) with *Zea Mays*, the latter being the pollen parent. The phenomenon of xenia was strikingly developed, the characteristics of the two genera appearing in the ears.—J. M. C.

Diseases of cereals.—BUTLER[26] has described four diseases of grasses in India caused by *Sclerospora graminicola*, the hosts being *Pennisetum typhoideum*, *Andropogon Sorghum*, *Setaria italica*, and *Euchlaena luxurians*.—J. M. C.

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[22] PEARSON, RALPH S., The level of subsoil waters with regard to forest. Indian Forester **33**:57–69. 1907.

[23] GOEBEL, K., Morphologische und biologische Bemerkungen.—17. *Nephrolepis Duffii.* Flora **97**:38–42. 1907.

[24] PERKINS, J., The Leguminosae of Porto Rico. Contrib. U. S. Nat. Herb. **10**: 133–220. 1907.

[25] VILMORIN, PH., *Reana luxurians* × *Zea Mays.* Bull. Soc. Bot. France **54**:39–42. *pl. 1* 1907.

[26] BUTLER, E. J., Some diseases of cereals caused by *Sclerospora graminicola.* Mem. Dept. Agric. India Bot. Series **2**^{1}: pp. 24. *pls 5* 1907.

NEWS

Professor Dr. Friedrich Hildebrand, Freiburg, has just retired from active service.

E. E. Bogue, professor of forestry in the Agricultural College of Michigan, died at Lansing, August 19, after a lingering illness, at the age of 42.

Dr. H. P. Lyon has resigned his position as assistant professor of botany in the University of Minnesota, to accept a position with the Hawaiian Sugar Planters Association at Honolulu.

Ginn and Company have announced *A manual of the North American gymnosperms* by Professor D. P. Penhallow. It is to be an account of the anatomy of the group, together with their systematic presentation on the basis of their vascular anatomy.

Professor J. E. Kirkwood has resigned his position at Syracuse University, having been appointed assistant to the International Rubber Co., with headquarters at Torreon, Mexico. Dr. W. L. Bray, University of Texas, has been appointed professor of botany at Syracuse.

Dr. H. N. Whitford, in government service in the Philippines, has been spending some months in the United States and has now started upon his return journey. A few weeks are to be spent in the Santa Catalina Mountains with a party from the Desert Botanical Laboratory.

Among the numerous Linnaean memorial addresses published recently, none is more interesting and sympathetic than the one delivered by Professor E. L. Greene at a joint meeting of the Washington Academy of Sciences, the Biological Society of Washington, and the Botanical Society of Washington. The citation is Proc. Wash. Acad. Sci. **9**:241–271. 1907.

Professor L. M. Underwood has published (Pop. Sci. Monthly **70**:497–518. 1907) a most interesting sketch of "The progress of our knowledge of the flora of North America," a sketch which should be read by the whole generation of younger botanists, who are in danger of remaining ignorant of the important history and of the great names that lie behind their present work. It is marred by uncalled-for slurs on some whose memory is to be held in highest honor.

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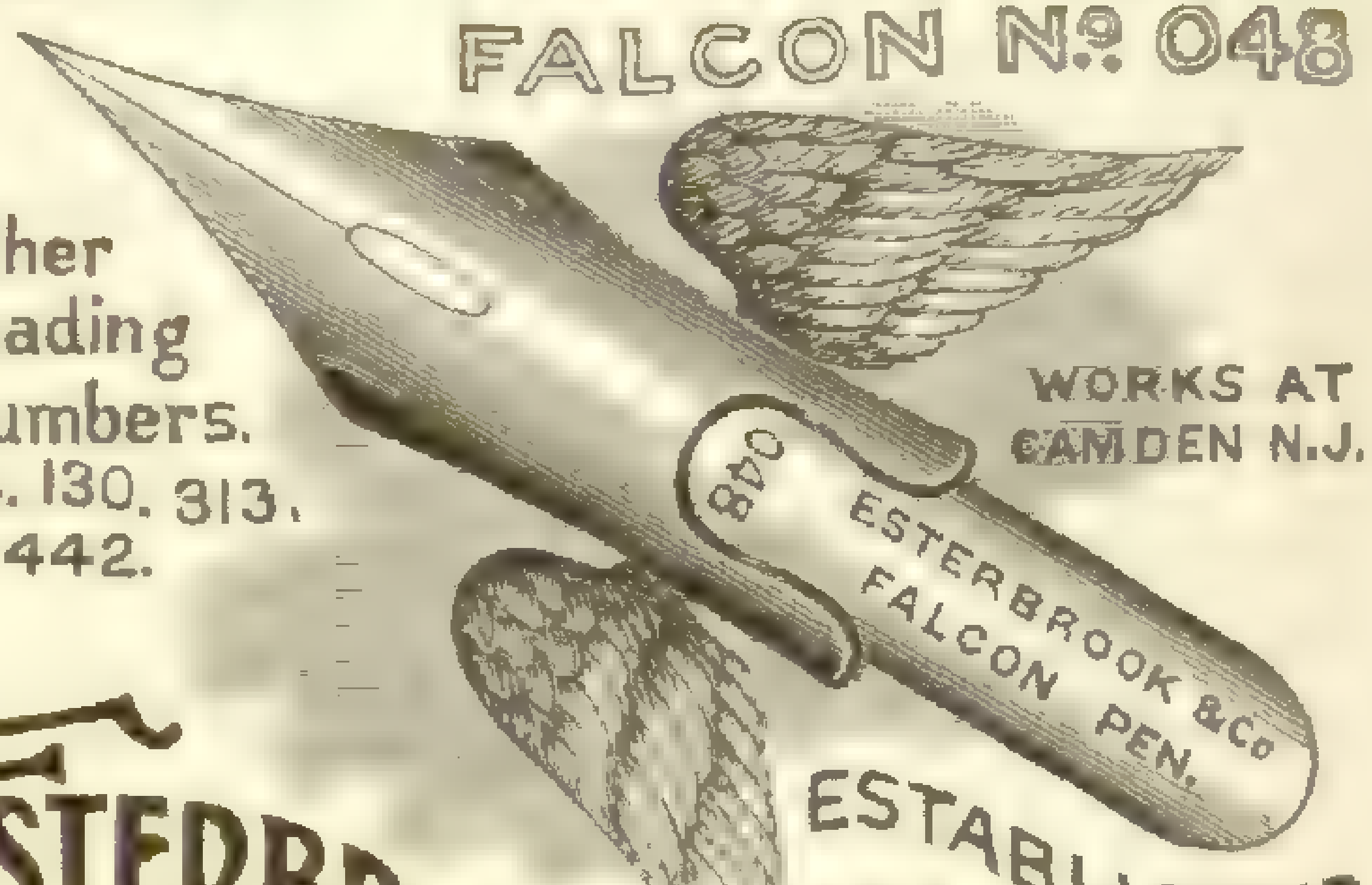

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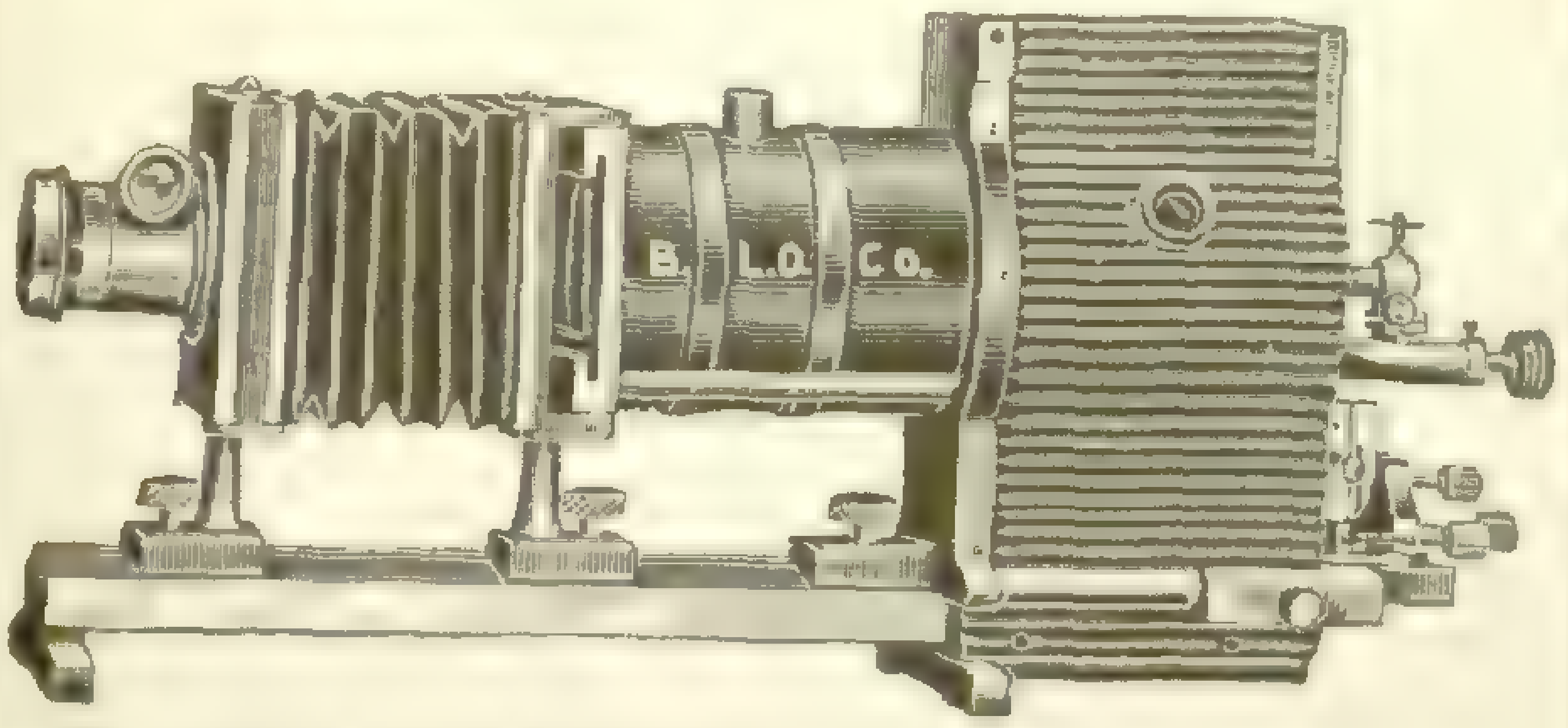

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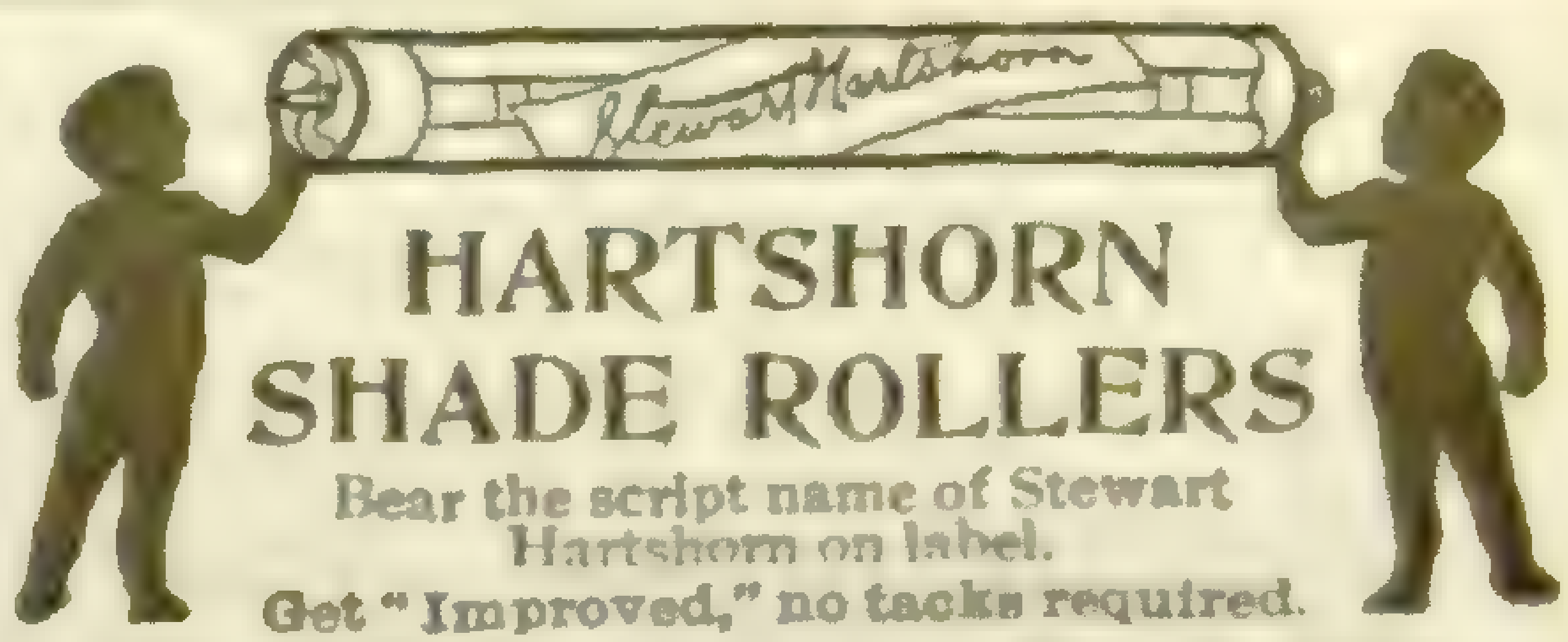

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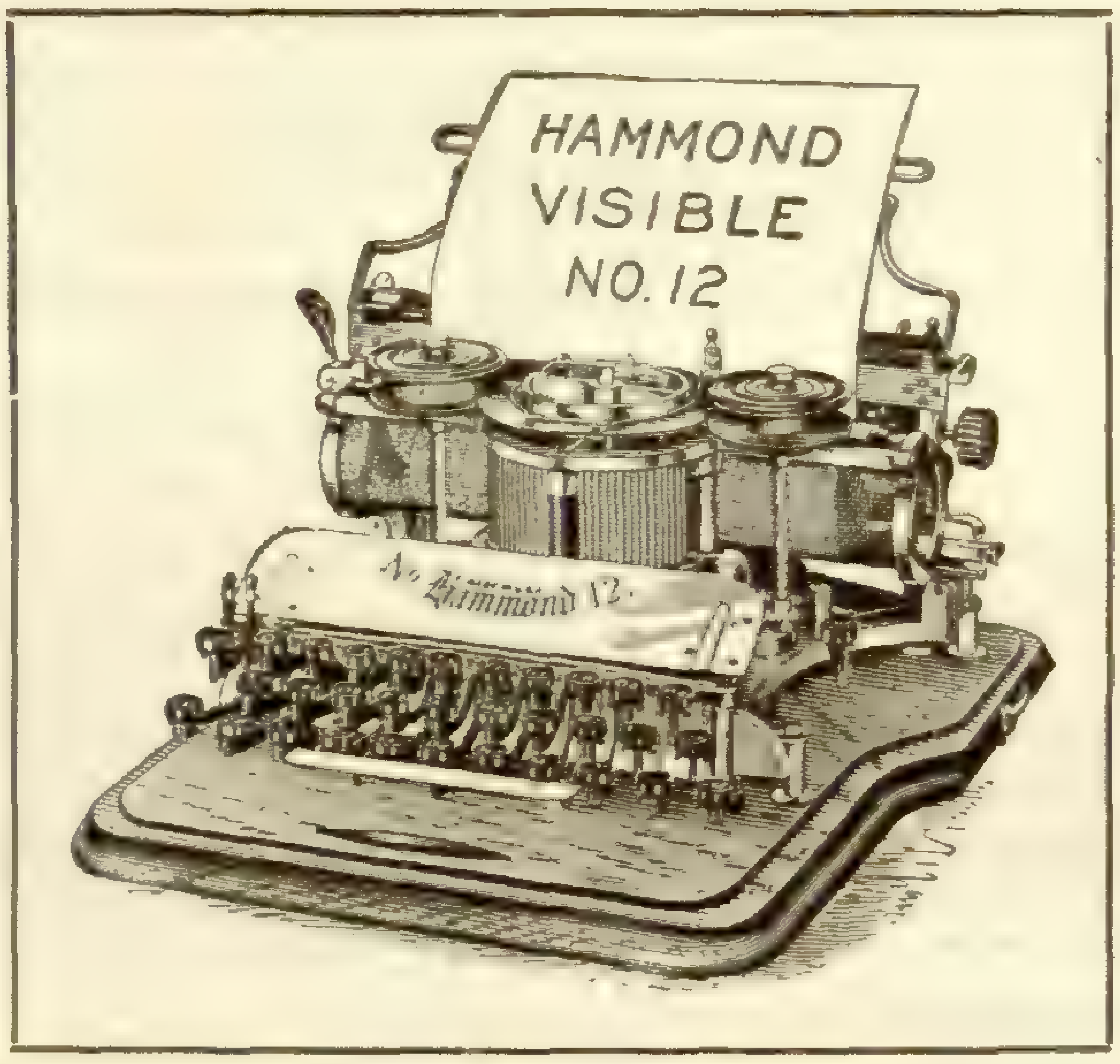

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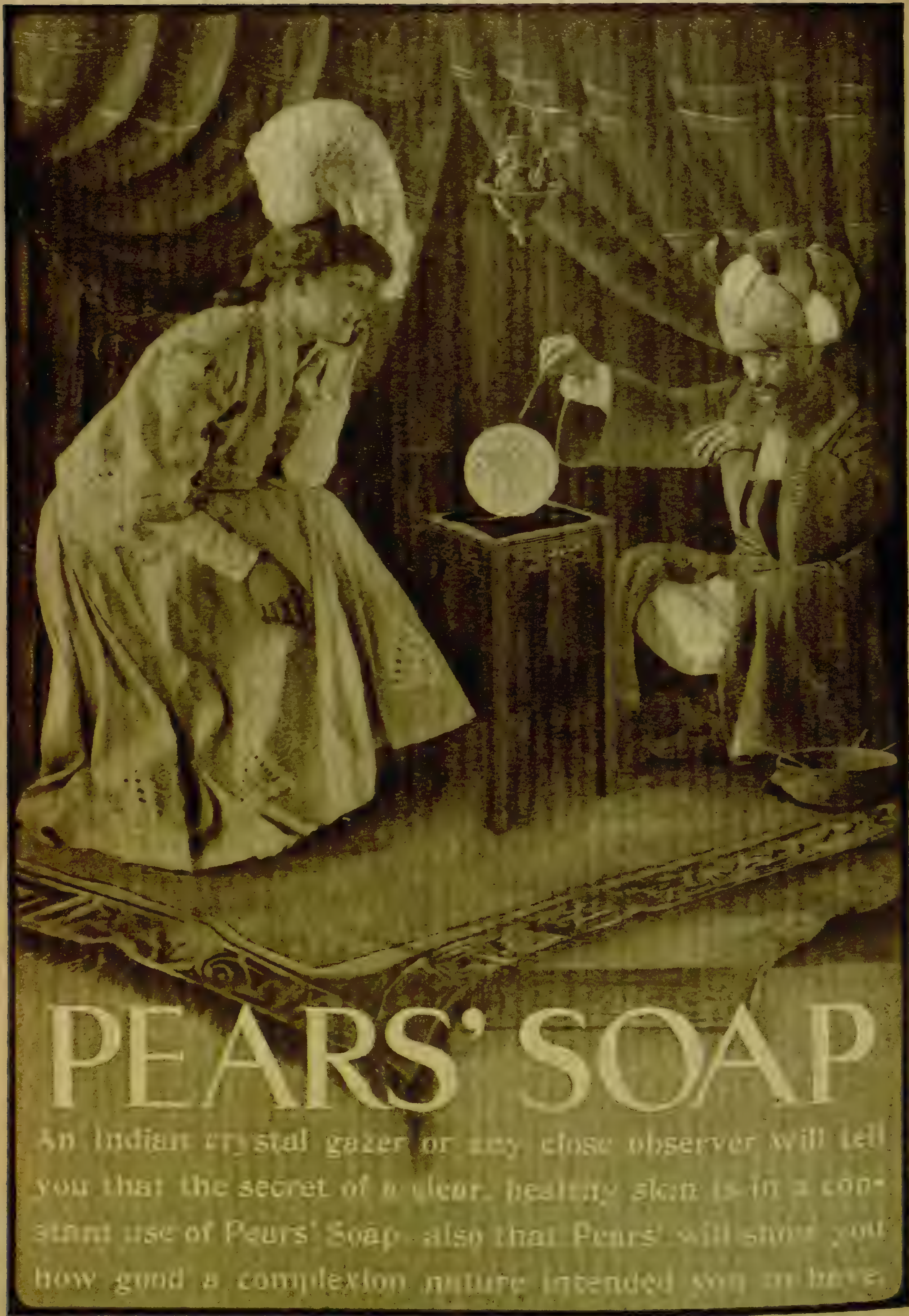

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Edited by JOHN M. COULTER and CHARLES R. BARNES, with the assistance of other members of the botanical staff of the University of Chicago.

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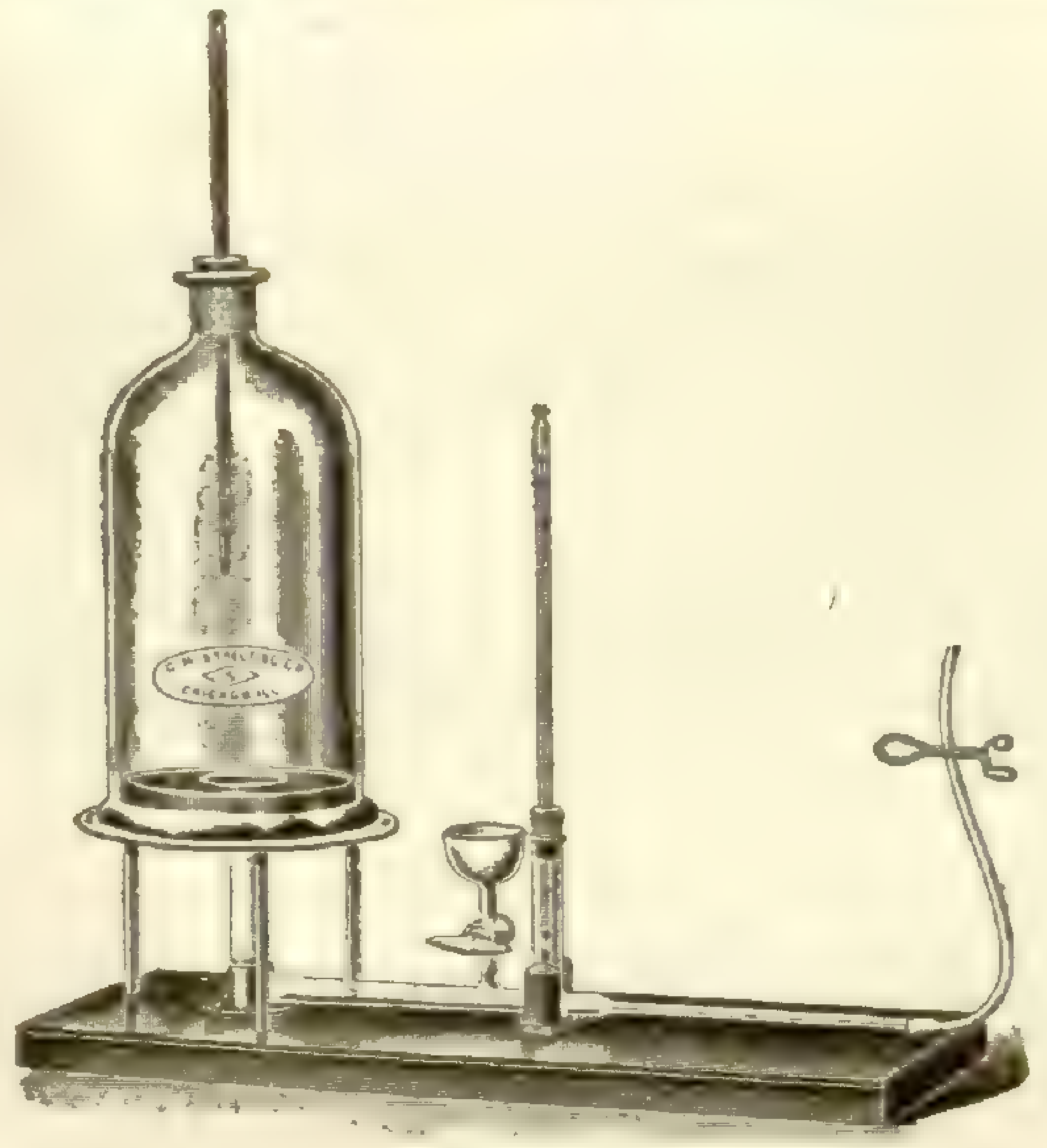

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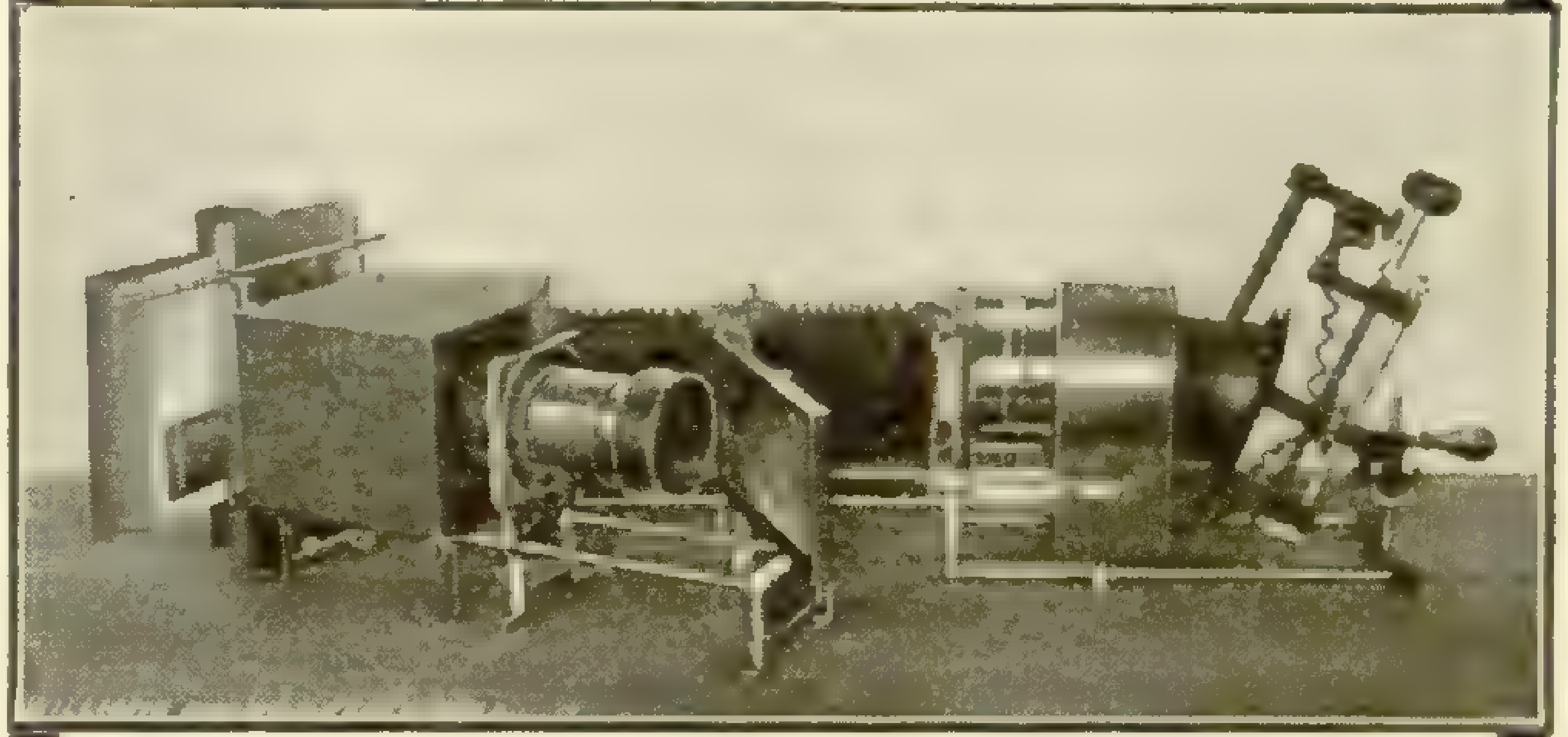

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VOLUME XLIV NUMBER 4

BOTANICAL GAZETTE

OCTOBER 1907

THE CHRYSANTHEMUM RAY BLIGHT[1]

F. L. STEVENS

(WITH FIFTEEN FIGURES)

The common name chosen for the disease at present under discussion is taken from the most conspicuous symptoms of the malady, a blighting of the corolla of the ray flower, resulting in poorly developed, discolored, one-sided heads (*fig. 1*).

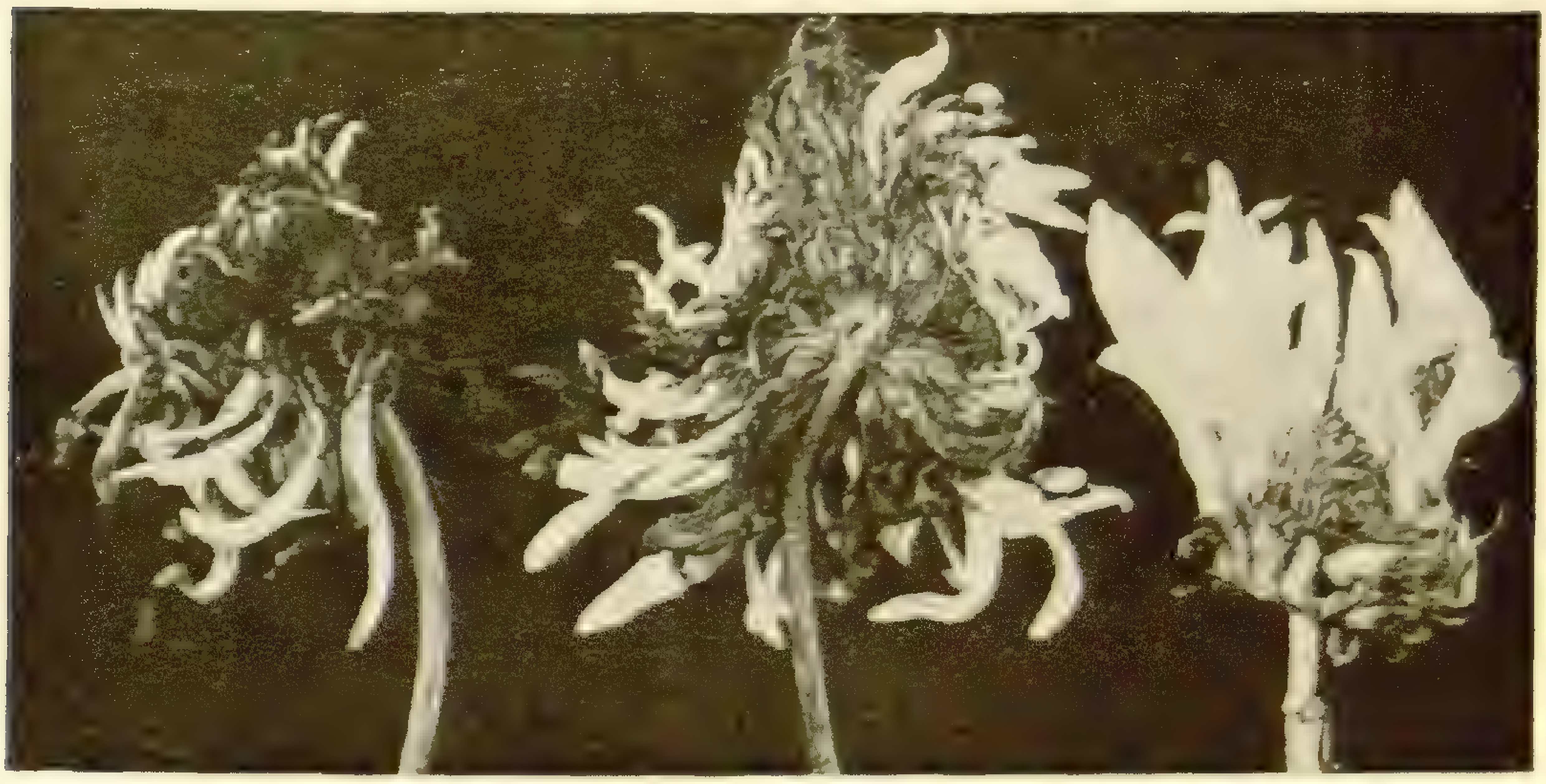


FIG. 1.—Three heads, showing disease as it naturally occurs.

Attention was first called to the disease by a letter from Fayetteville, N.C., dated November 13, 1906, and accompanied by specimens. The disease has been known at that place and has recurred for three years, each year with increasing destructiveness. It was first attributed by the owner of the plants to want of ventilation, but upon its recurrence the second year, the possibility of such a cause was precluded by the conditions. The disease was found upon plants in the open as well as upon those of the greenhouse. The first year it was found only upon late varieties, but this year it appeared upon all varieties in the owner's collection, the variety "Nellie Pockett" being particularly susceptible. The "Golden Wedding," a late yellow variety, always suffers badly in the collection in question. Since receiving the specimens from Fayetteville the disease has been found in Raleigh, and it may be of wide distribution.

---

[1] Contribution from the Laboratory of the North Carolina Agricultural Experiment Station, Raleigh, N. C.

SYMPTOMS

The disease is most conspicuous in the flower clusters, which it attacks usually upon one side, either in the bud or during various stages of blooming. The affected blossoms turn straw color or brownish, cease to develop, and wither, the discoloration proceeding from base toward tip on each individual flower, thus distinguishing the disease at once from many disorders which may resemble it superficially. If the case be severe, and a bud be attacked while still young, no rays will develop; the head will not open. If the attack be later, a portion of the head, one-half or two-thirds, or more or less, may develop normally and thus by contrast heighten the conspicuousness of the disease. Heads nearly open and apparently healthy may on the following day show one side far advanced in disease. The owner says, "it developed so fast that a large perfect bloom in the morning would be wilted by night."

The receptacle turns black, and the peduncle may likewise be blackened to a distance of one or two centimeters below the head. Later, shriveling and softening of the peduncle allow the head to nod in a characteristic manner.

On the affected plants the stems are often blackened for several centimeters, in a band more or less completely encircling the stem. Frequently this diseased region is associated with a leaf, the petiole of which also partakes of the discoloration.

MICROSCOPIC EXAMINATION

Under the microscope, diseased flowers, rays, corollas, receptacles, peduncles, and the diseased portions of the stem all reveal the presence of a rather coarse, much branched mycelium that is easily recognized by its septa, which are numerous and stand out with an especially striking clearness (*fig. 2*). In the humid region between the flowers in the head, the mycelium becomes aerial, forming a loose floccose weft, visible to the naked eye. In the pith cavity of the blighted receptacle a similar profuse mycelial development occurs; while on old specimens, in culture dishes, pycnidia were also found identical with those which developed in the pure cultures to be described later (*fig. 3*). Only one fungus was seen and no bacteria whatever were visible.

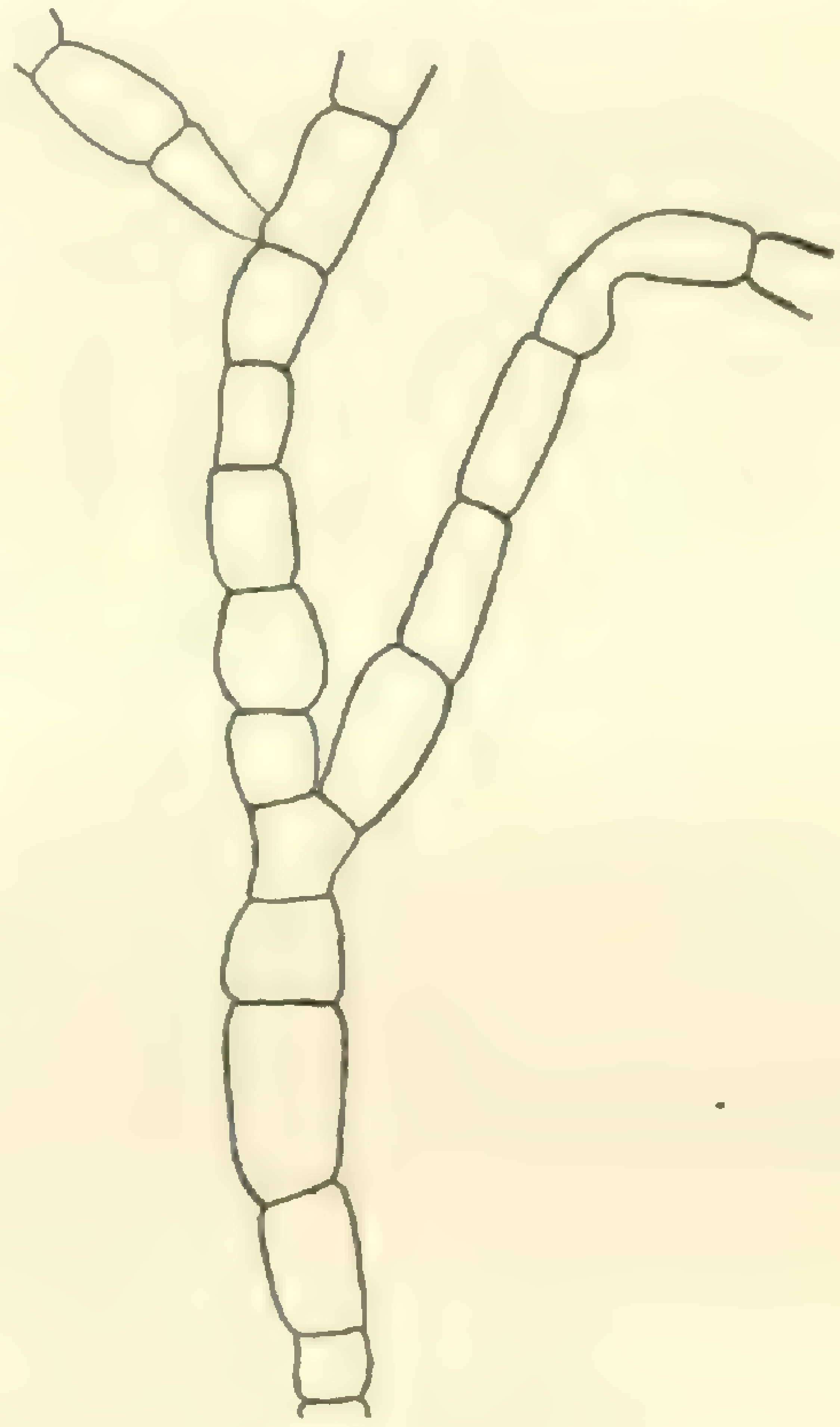


FIG. 2.—Normal hyphae, mature, showing septation with slight constriction; also the mode of branching.

ISOLATION

Diseased ray flowers were removed with sterile forceps and thrown upon solidified pea agar in Petri dishes, several to each dish. Similarly, with aseptic precautions, bits of the wood and bark from diseased peduncles, stems, and from the inside of the receptacle were plated. Each of these cultures, 25 or more in number, plated on November 18, resulted within 24 hours in pure colonies, all alike, of a fungus with a mycelium identical in appearance with that seen in diseased tissue.

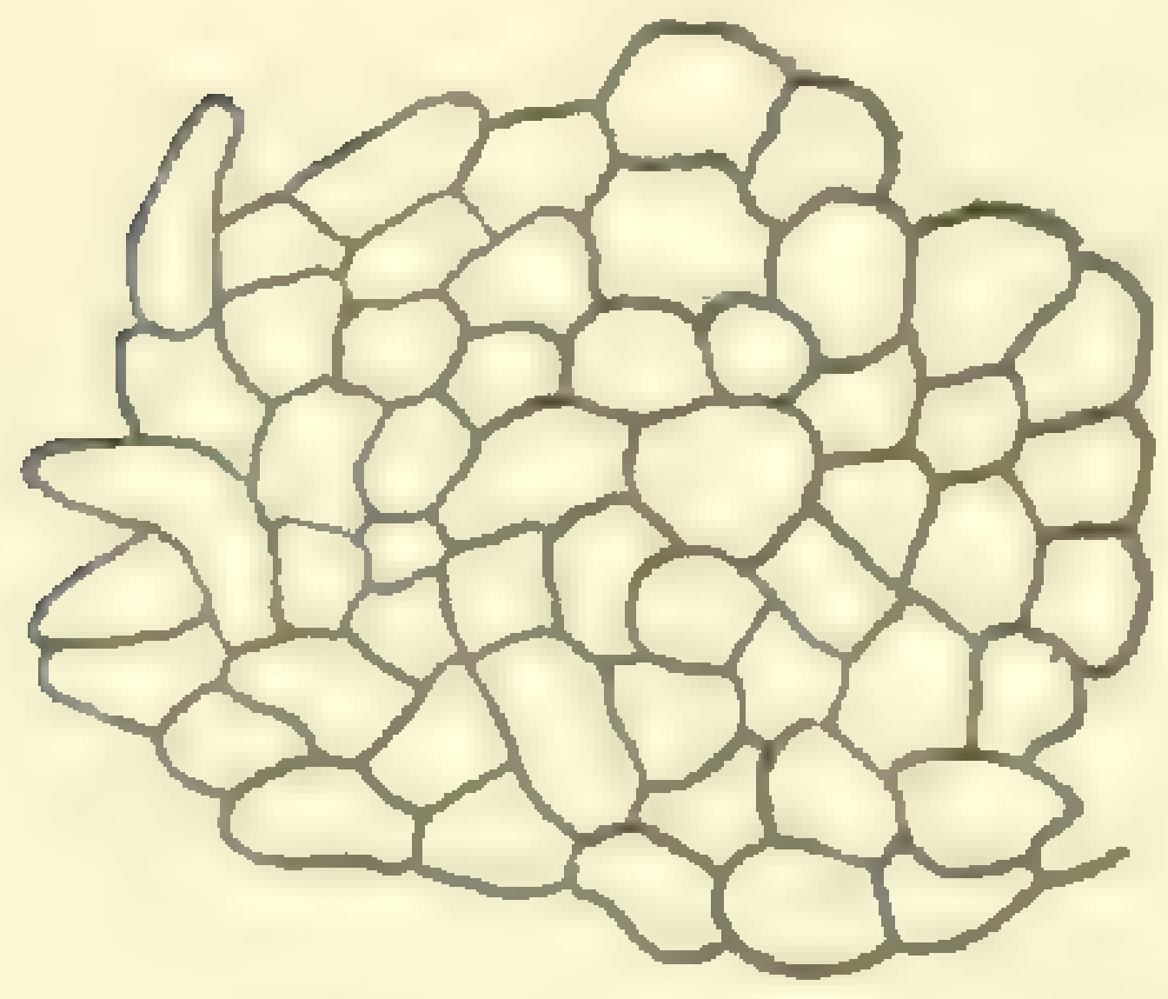


FIG. 3.—Surface view of pycnidium showing reticulation.

THE FUNGUS

The colonies grew with remarkable rapidity and remained sterile until five days old. Pycnidia were found then in the oldest portions of a colony upon one of the plates. They were amber color, as seen with the two-thirds objective and transmitted light approaching no. 30 of SAC-

CARDO's *Chromotaxia*, or the YYO[4] of the PRANG *Standard color scale*. They were coarsely reticulated on the surface (*fig. 3*), owing to their composition of woven, coarse, mycelium threads. In diameter they ranged from 102 to 204 μ (the most usual size being about 150 μ). They were round in outline and elevated from the surface, hemispherical. Grown upon corn and also upon the apple agar, the pycnidia were very much darker, almost black. The ostiolum seemed entirely absent in many pycnidia which developed deep in the culture medium, but was present in all growing upon the surface of artificial media or upon natural substrata.

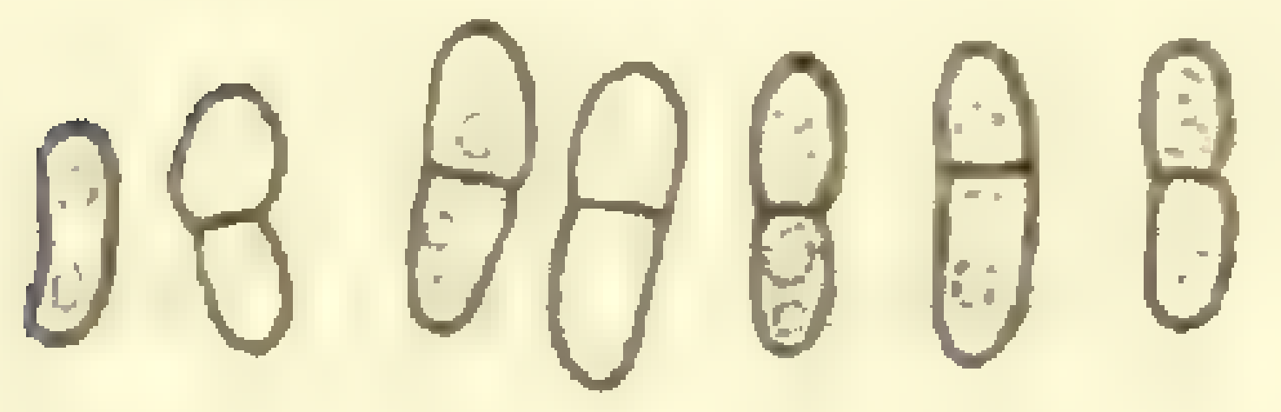


FIG. 4.—Spores from pycnidia grown on cow pea agar.

The spores are regular and oblong, or quite irregular-oblong, or swollen and rounded at one end and pointed at the other. Regular-oblong, however, is the prevailing type, with a pronounced tendency to irregularity (*fig. 4*). One septum, more easily seen in stained preparations, is visible in most of the older spores; though young or small spores and many larger older ones do not show it. The septum is frequently central, but there is a tendency for it to be located

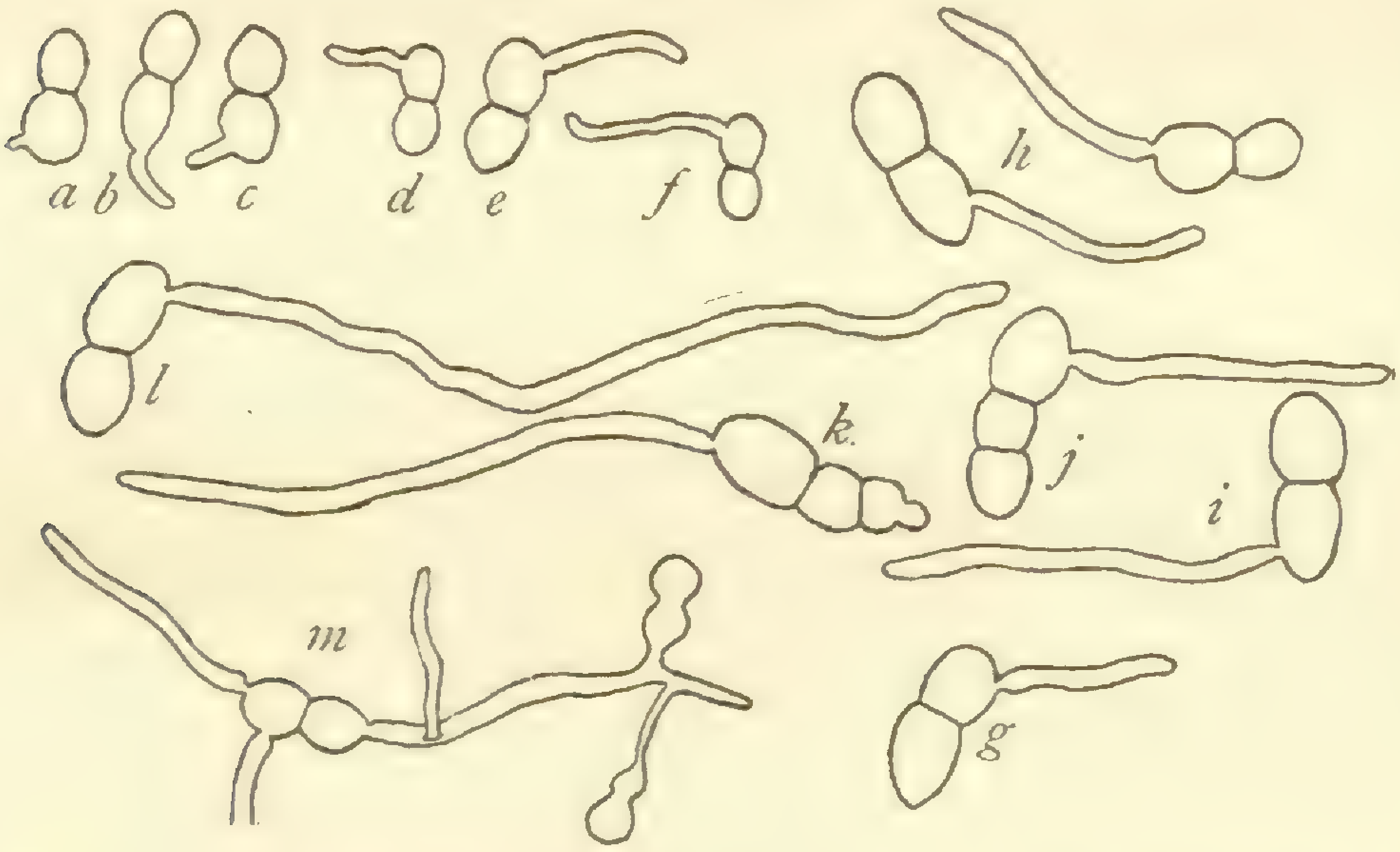
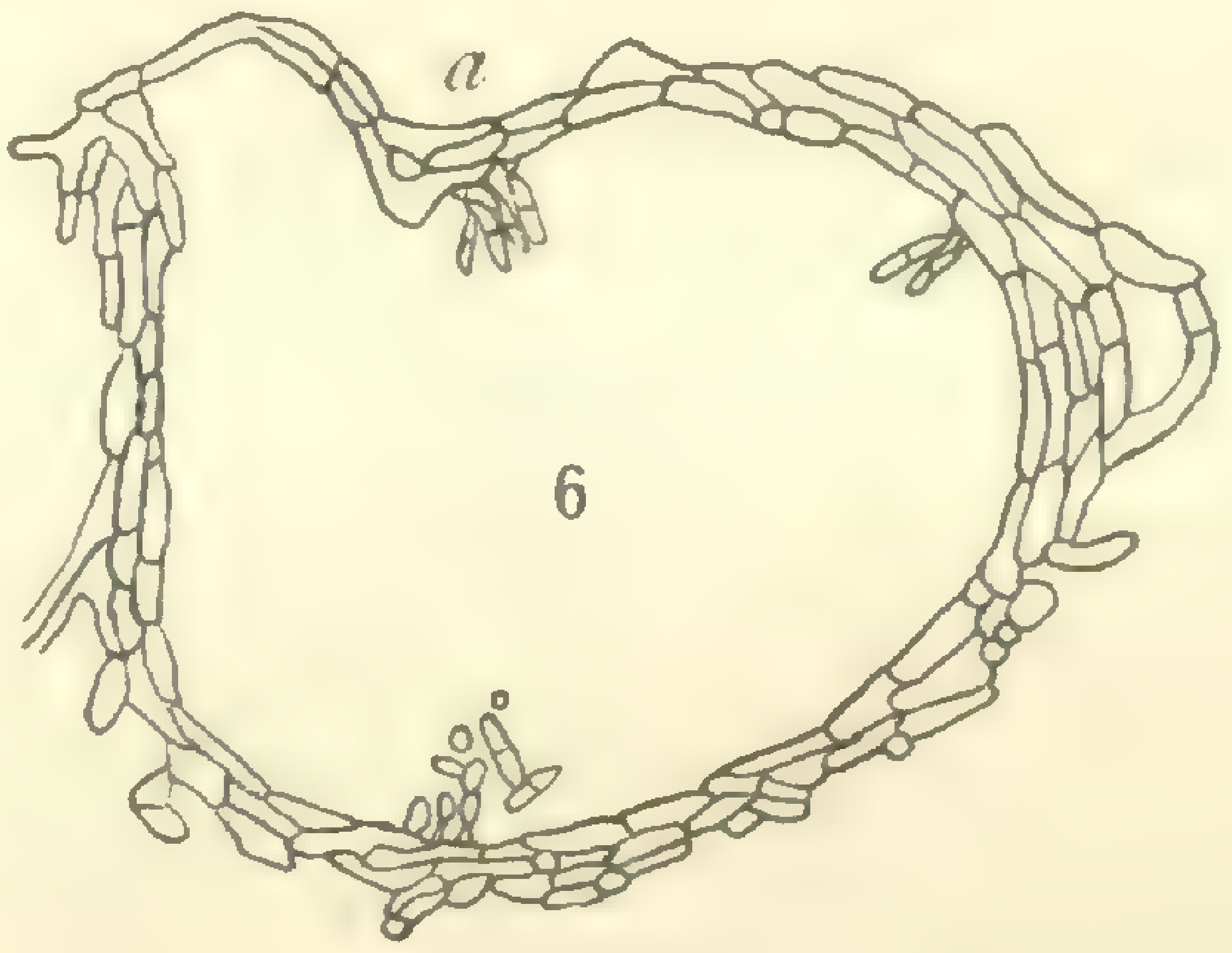


FIG. 5.—Stages in the germination of spores; *e* and *f*=*c* and *d* respectively, drawn one hour later; *c* and *d* drawn at 6 hours of age, and *e* and *f* at 7 hours; *m* 15 hours old.

nearer to one end than to the other. Rarely two septa or even three are present in one spore. The spores measure from 3 to 6.2 μ in thickness by 10 to 20 μ in length; 6.2 μ by 18 μ being the usual size. The spores are hyaline or very slightly greenish. In mass, as extruded from ripe pycnidia, they appear slightly pink. The walls are evidently mucilaginous, since the spores, as they are pushed from the pycnidia upon the absorption of water, issue in wormlike coils, cohering thus for considerable time, though they are not in visible contact. The spores germinated rapidly in water (*fig. 5*), practically every spore germinating. In germination the septum appeared in all spores, and one to three germ tubes protruded from each cell. These tubes rapidly became richly septate, and the protoplasm highly vacuolate.



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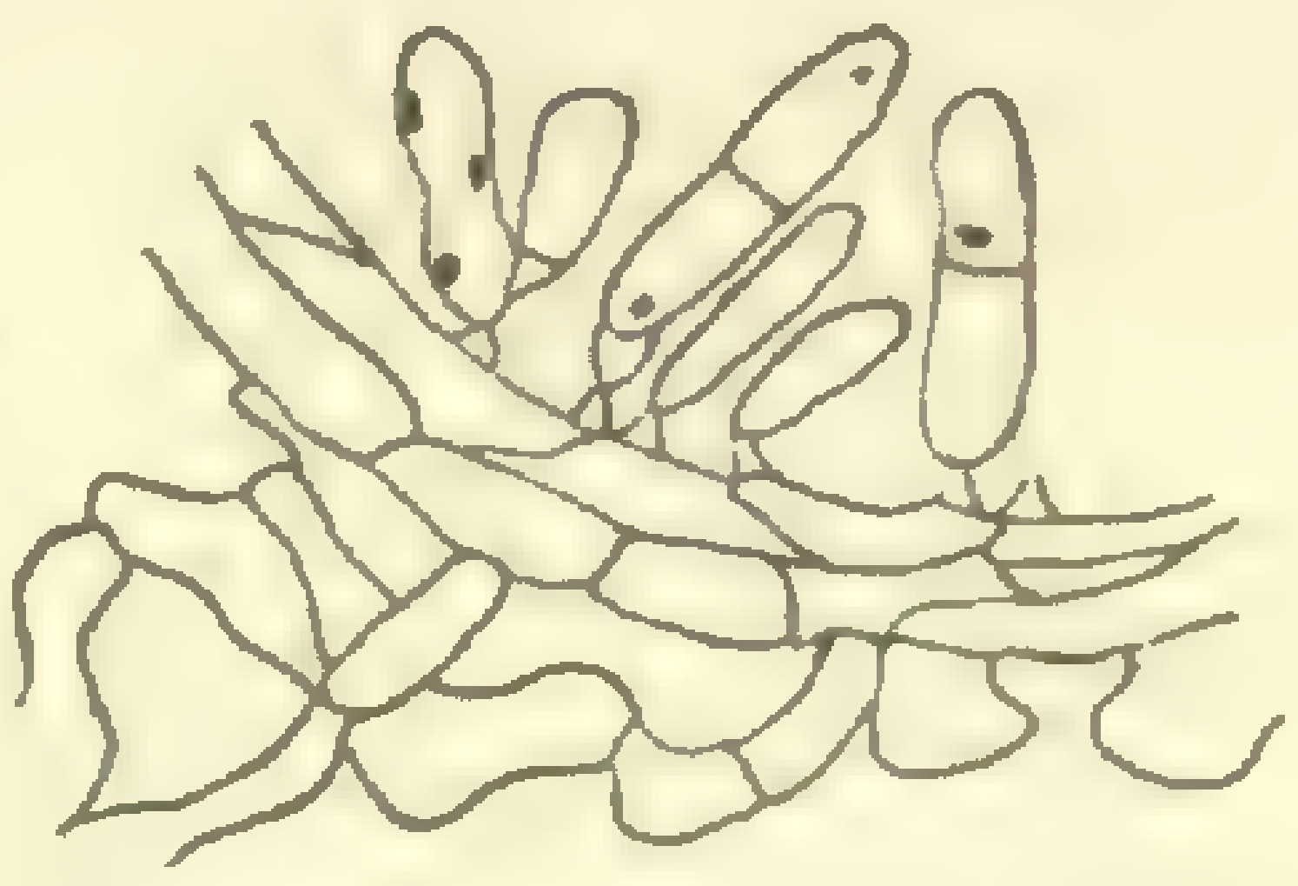

FIG. 6. Section of pycnidium. *a*, neck of ostiolum.—FIG. 7. Portion of pycnidial wall in section showing method of spore attachment.

In sections (*fig. 6*) the spores are seen to be borne on all inner portions of the pycnidial wall except the very short neck of the ostiolum, each spore originating singly (*fig. 7*) on the end of a very short stalk (about 2 to 5 μ long). These sporophores are lateral branches of the mycelial threads which constitute the pycnidial wall. The pycnidium originates within the host tissue, i. e., immersed, but rapidly enlarges to burst the overlying epidermis, so that the mature or even half-grown pycnidium appears to be superficial. There is no special aggregation of mycelium to be found below the base of the pycnidium.

The very young pycnidium is solid. Later a spore cavity develops, though apparently no more rapidly than is necessitated by spore production. In the youngest pycnidia having a spore cavity, the surrounding wall is composed of several (five to eight) layers of mycelium. As the spore cavity becomes distended the wall becomes thinner, until at maturity it is composed of only one, two, or three layers of mycelium, while the region of the ostiolum becomes one layer thick and eventually ruptures.

This fungus clearly belongs to the section HYALODIDYMAE Sacc. of the SPHAERIOIDEAE Sacc. and seems closest in affinity to the members of the genus *Ascochyta*. The possession of a slight beak, which however is always very small and often entirely absent, might throw it into the genus *Rhyncophoma* Karst., but members of that genus are typically upon wood, usually saprophytic, and have a more pronounced beak.

Since no Ascochyta, or indeed any other species of the Sphaerioideae Hyalodidymae, which could by any possibility be identical with the species considered in this paper, has come to my notice as growing upon the chrysanthemum or any of its kin, I regard this as a new species, for which I give the following description.

Ascochyta Chrysanthemi, n. sp.—Perithecia few, immersed, early erumpent, single or scattered, round, hemispherical, amber colored, 100–200 μ, mostly about 150 μ; ostiolum central, small, dark bordered, often raised by a short neck; surface reticulate, pycnidia on agar media irregular, often with two ostioles and varying much in size, black in color. Mycelium abundant, innate, also superficial, aerial, floccose, richly septate.

Spores oblong, straight or irregular, 3 to 6.2×10 to 20 μ, mostly 6.2×10 μ, ends obtuse or acute; septum usually one, often obscure, rarely 2 or 3, usually without constriction until germination; protoplasm vacuolate, hyaline or light pink in mass.

HABITAT: in corollas, heads, petioles, and stems of cultivated plants of *Chrysanthemum indicum*, causing blight. North Carolina.

CULTURE CHARACTERISTICS

Thermal relation.—Cultures in Petri dishes on cow pea agar were placed in darkness at three temperatures with the results appearing in the adjoining table.

The growth both outdoors n the cold, and in the incubator, was exceedingly irregular, stunted, or slow, while that of room temperature was very much more rapid.

In addition to being an unfavorable temperature for growth, the heat of the incubator produced great irregularity in the zonal development; threads started vigorously, stopped suddenly, and growth began in another direction, so that all regularity of zone formation was lost. Much of the mycelium also became incased in a dark coat, as described under the effect of cow pea leaf agar below. The plates kept at outdoor temperature, while they maintained a fair regularity in the formation of zones, did not make the same number of zones as the cultures kept at room temperature, the number of zones made in the room temperature being six while that outdoors was four.

Acid relation.—Cultures in lettuce agar in the dark at room temperature in various degrees of acidity gave the record shown on Table II on the following page:

TABLE I

INOCULATED DEC. 8, 1906. GROWTH IN MM.

December	9	10	11	12	13	14	15	16	17	18	19	Daily average
In room												
Temp. max./min.	—/—	—/—	12/20	12/20	18/21	17/21	18/20	—/—	12/18	—/—	11/17	16.19
Plate 1..........	2	4	—	12	15	18	22	25	26	33	39	3.5
Plate 2..........	2	3	—	12	15	18	22	25	26	33	39	
In incubator												
Temp. 30–35°												
Plate 35.........	3	3			contaminated							.2.2
Plate 36.........	3	3		?	?		8	11	15	22	25	
Outdoors												
Temp. max./min.	3/17	10/18	1/14	3/7	1/16	6/22	9/22	10/21	22	14/14	—/—	—/—
Plate 37.........	0	2		?			7	11	14	19	22	2.0
Plate 38.........	0	2					7	11	14	19	22	

TABLE II

INOCULATED DECEMBER 13. GROWTH IN MM.

Plate	Drops of normal acid or alkali per tube	Fuller's scale	14	15	16	17	18	19	Average per day
25....	acid 10	+40	?	0	0				
27....	acid 5	+20	?	0	0				
49....	0	0	2 growth	3	7	12	15	18	3.1
31....	alkali 5	−19		3	5	11	14	16	2.6
29....	alkali 10	−39	?	2	3	8	9	10	1.6
34....	alkali 15	−59	?	0	0	2	3	4	.7
33....	alkali 20	−99	?	0	0	gr.	5	6	1.

It is clearly seen from these data that a neutral medium or one only slightly alkaline favors the growth of this fungus.

In the plates with 10, 15, and 20 drops of normal alkali there was no formation of zones at all. In the plate bearing 5 drops of alkali two zones were formed.

The four cultures inoculated December 8, grown at room temperature, two in light and two in darkness, agreed almost absolutely in rate of growth, a total difference of 1 or 2^{mm} noted at the end of ten days' growth being so small as to be insignificant.

Growth in various media.—Cultures in agar with various nutrients at room temperature in the dark grew as follows:

TABLE III

INOCULATED DECEMBER 13, 1906. GROWTH IN MM.

Plate	Medium	Dec. 14	Dec. 15	Dec. 16	Dec. 17	Dec. 18	Dec. 20	Dec. 21	Jan. 12
		17–21°	18–20°		12–18°				
9...	Pure agar	Grew	4	6	11				65
10..		"	4	7	11	14			70
7...	Pea agar	"	4	6	10	13			18
8...		"	4	6	10	14			18
15..	1% peptone	"	3	5	9	9			70
16..	agar	"	4	7	10	11			70
11..	1% glucose	"	5	9	15	19			80
12..	agar	"	5	8	13	17			80
13..	5% glucose	"	6	11	16	21			70
14..	agar	"	6	11	16	21			75
17..	1% starch	"	4	6	10	11			
18..	agar	"	4	7	11	12			

Plate	Medium	Dec. 8	Dec. 9	Dec. 10	Dec. 11	Dec. 12	Dec. 13	Dec. 14	Dec. 15	Jan. 12
					12–20°	12–20°	18–21°	17–21°	18–20°	
5...	Standard	Grew	1.5	2	5	9	10	11	14	52
6...	beef agar	"	1.5	2	5	10	12	13	15	32
3...	Cow pea	"	2	3	5	12	14	18	22	
4...	agar	"	2	3	5	12	14	18	22	
39..	Standard	"	2	2	4	6	8	11	15	35
40..	beef gelatin	"	2	2	4	6	10	12	15	..

Colonies grown in *pure agar* in dark or light and those upon pea agar were of the same general appearance, thin, colorless, and structureless, zone formation being entirely absent. A very few pycnidia were produced. By increasing the richness of the pea agar to 4 per cent., pycnidia were secured, but without change in other characters. The growth in pea agar was no more rapid than that on pure agar, but was much more dense; the mycelium was colorless and very few pycnidia developed.

One per cent. *peptone* adds nothing to the nutrient value of the medium for this fungus. Growth comes to an end earlier than in pure agar or other media; there are no pycnidia, no color to the mycelium, and only a very slight indication of zonation.

Glucose, 1 and 5 per cent., favor growth, the five per cent. being slightly better than the one per cent. No pycnidia developed, but there is marked, though irregular, zonation in both darkness and light, and the whole mycelium develops a striking, intense blackness. The septation and cell contents are normal and the color rests with the cell wall.

Starch, 1 per cent., did not increase the rate of growth, although upon microscopic examination it was clear that the starch grains were digested almost as soon as the advancing threads of the fungus reached them, and growth continued long in these plates. The effect of starch upon the general appearance of the colony and upon the mycelium was precisely as in the glucose plates.

In *standard beef agar* and *gelatin,* growth was about as with peptone agar, though it continued for a longer time. The mycelium was of abnormal, irregular character (*fig. 8*), and there were no pycnidia nor any development of color nor of well-marked zones.. On *beef* *gelatin* the growth was more uniform than on beef agar, and the zones were somewhat clearly marked, liquefaction following in the wake of the mycelium, lagging about 4 or 5^{mm} behind the mycelial tips.

In *litmus lactose agar* the colonies developed as on beef agar without acidity.

Upon *cow pea leaf agar* the growth, while exactly parallel in rapidity with the growth upon the cow pea agar, exhibited remarkable differences in the structure of the colony, the number of zones being much less and the breadth consequently much greater. The mycelium also clung closer to the medium, was less floccose and less aerial, and in the older region of the mycelium the cells became extraordinarily thick and short and assumed a dark color. In some instances the protoplasm within the cell rounded off and became invested by a thick brown coat. In other instances a similar brown coat of much greater thickness, often four or five times as thick as the diameter of the mycelium, would form around the mycelial threads (*fig. 9*). Cow pea agar proved the best medium for the growth of this fungus. The

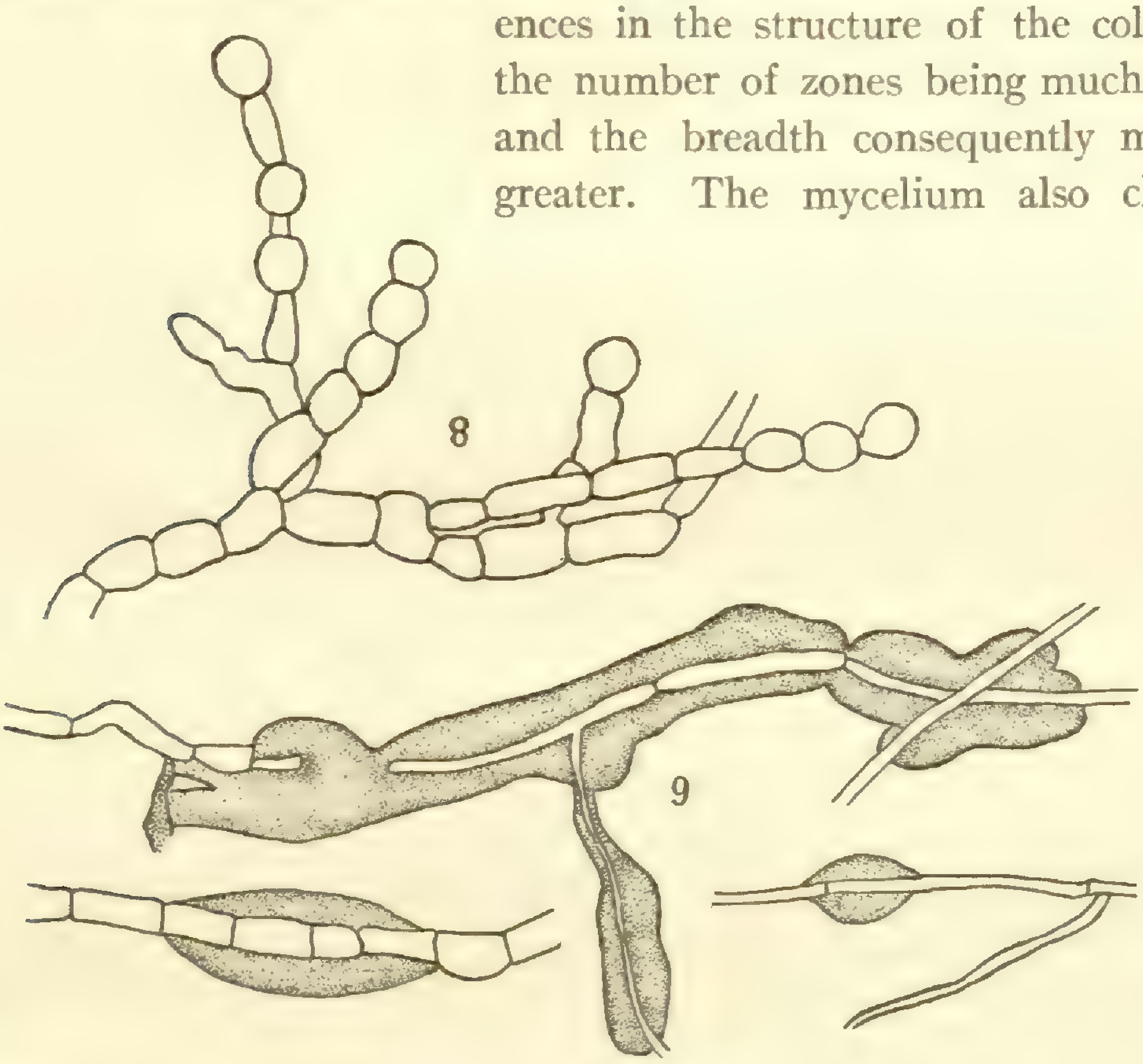

FIG. 8. Abnormal hyphae, mature, as grown in gelatin, the cells being unusually swollen.—FIG. 9. Thickening of hyphae, produced by too high temperature or an excess of nitrogenous food.

concentric zones formed with great regularity, five dense zones and six lesser zones being formed in a period of eleven days. In the older central portion pycnidia began to form at the end of about eight days, though often later. Pycnidial formation proceeds from the central zones to the younger zones, the pycnidia being most numerous in the denser zones, although they are by no means lacking in the lesser zones.

Upon *boiled rice,* in test tubes, the fungus grew luxuriantly. As the threads first invaded the rice there was developed a salmon color, which later turned to black.

Upon *boiled corn,* in test tubes, the mycelium developed well, became black, and pycnidia were present in abundance at the end of eleven days.

The most striking features noted in these nutrition studies were the influence of starch and glucose in agar or the starch of the rice or corn media in causing the development of an intense black coloration in the mycelium; and the unfavorable influence of peptone, beef, and gelatin as evidenced by distorted mycelium and the failure to develop pycnidia.

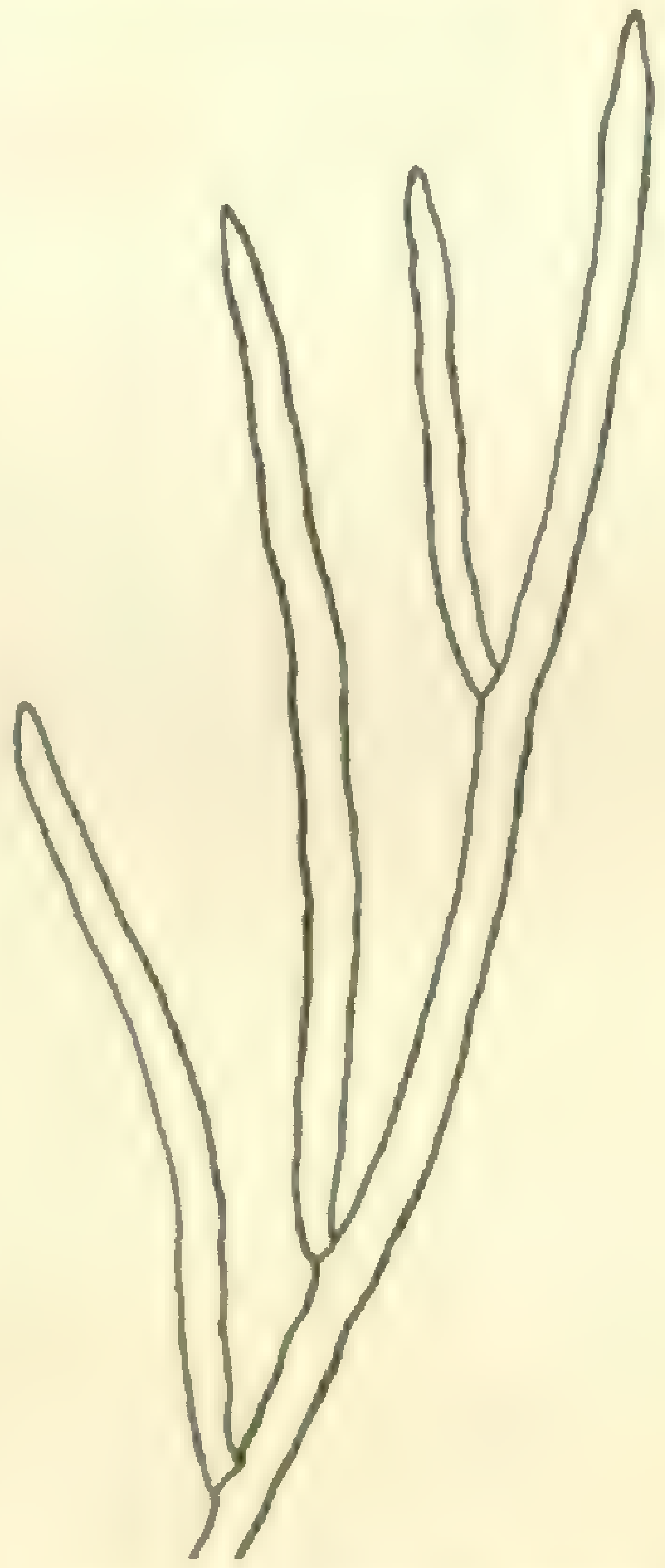
FIG. 10.—Tips of young rapidly growing hyphae.

The *formation of zones* is the most characteristic feature of growth of this fungus upon clear, solid media (*fig. 11*). Reference has constantly been made to this feature. The lesser zone, the zone which immediately surrounds the point of inoculation, is due to the mycelium growing out rapidly in every direction from the point of inoculation. As each individual thread becomes more and more distant from the center and has made more and more branches, the threads begin to crowd each other much more closely until, if conditions be proper, a time is reached when apparently the crowding becomes so great that further growth in length is inhibited. There then occurs a development of aerial hyphae and a thickening and darkening of the ends of hyphae already produced; this results in a darker zone surrounding the lighter zone. After maintaining this condition for some time, individual threads, in a scattered fashion, break through the outer dense zone, continue their growth, and proceed to the formation of a second lesser zone, followed in course of time by a second denser zone, all being formed in precisely the same fashion that the first two zones were made. Plates have been exposed under different light relations and different temperatures, and it seems probable that there is no connection between either of these factors and formation of zones in this fungus, other than is occasioned by increasing or decreasing growth.

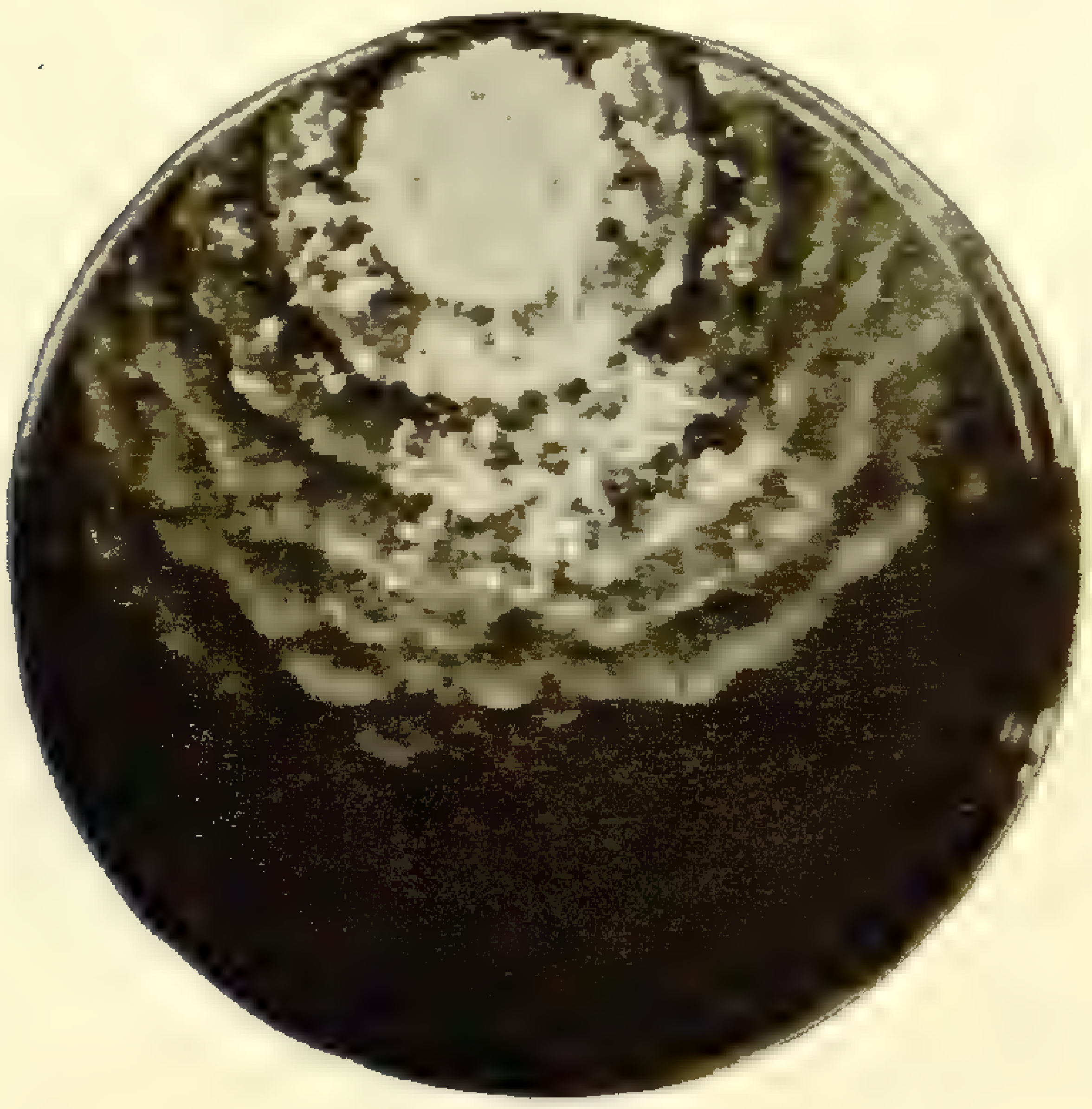

FIG. 11

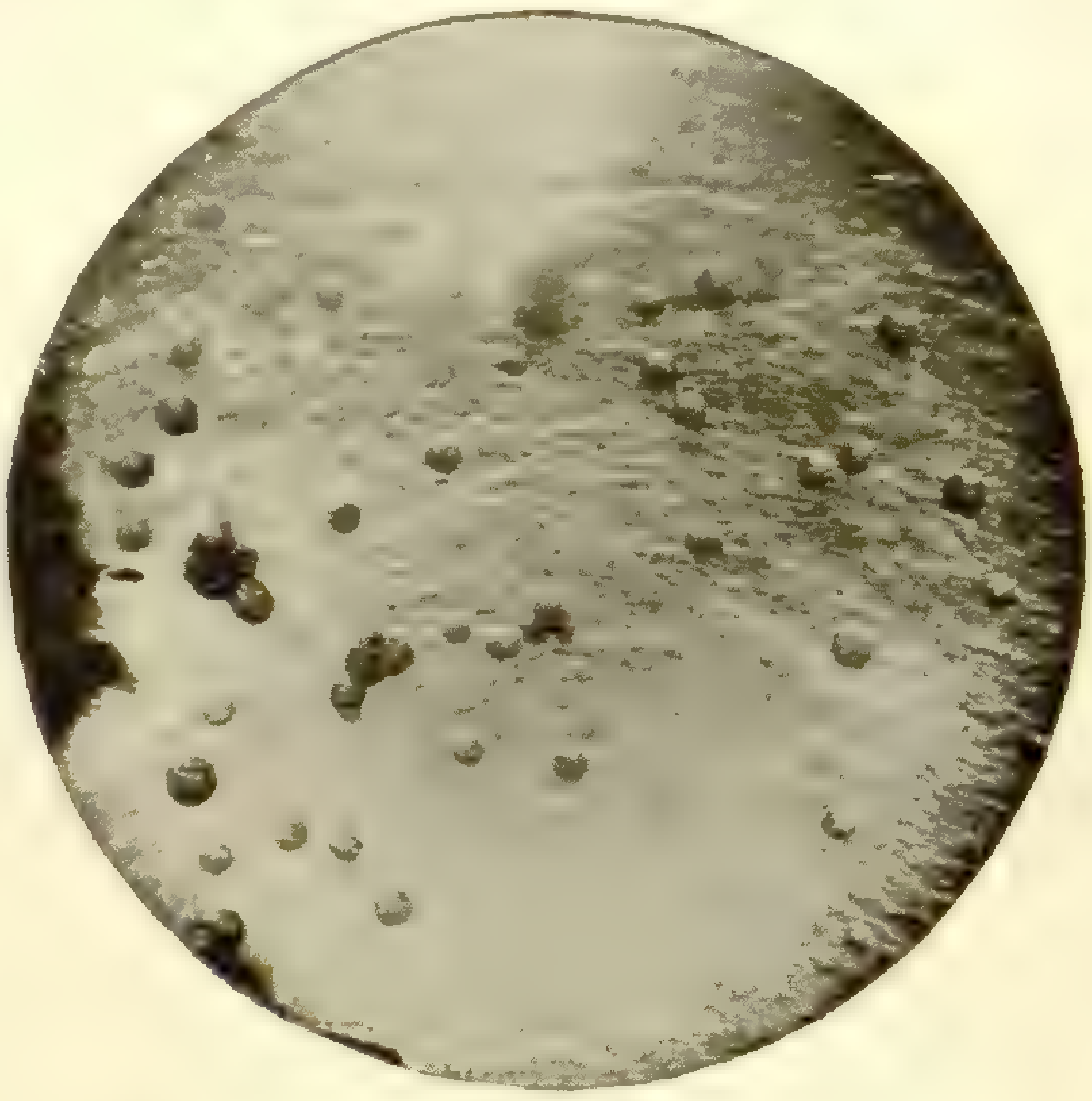

FIG. 12

FIG. 11. Pure culture of the fungus 17 days old, grown upon cow pea agar in diffuse light; pycnidia not then formed.—FIG. 12. Pycnidia on agar plate, viewed from below.

INOCULATIONS (*figs. 13, 14*)

Some forty inoculations were made with mycelium taken from pure cultures on bits of agar. Of these twenty-eight gave positive results. Control cultures remained uninfected. Inoculations were made within the involucral scales, between the flowers in the head, on stems, and on leaves, as follows:

Series I

Inoculated from mycelium obtained from the original agar plate culture on which diseased rays had been placed. Inoculations made November 22, 1906.

Inoculation no. 1: under the involucre of the bud which was just beginning to open; December 8, growth observed; December 18, exhibited typical disease.

Inoculation no. 2: in the axil of the uppermost bract, in needle pricks, with agar; the bud above was just beginning to open; examined December 8 and 18 with no indication of disease.

Inoculation no. 3: with mycelium upon agar upon the end of the unopened bud; examined December 8, no growth; December 18, typical disease.

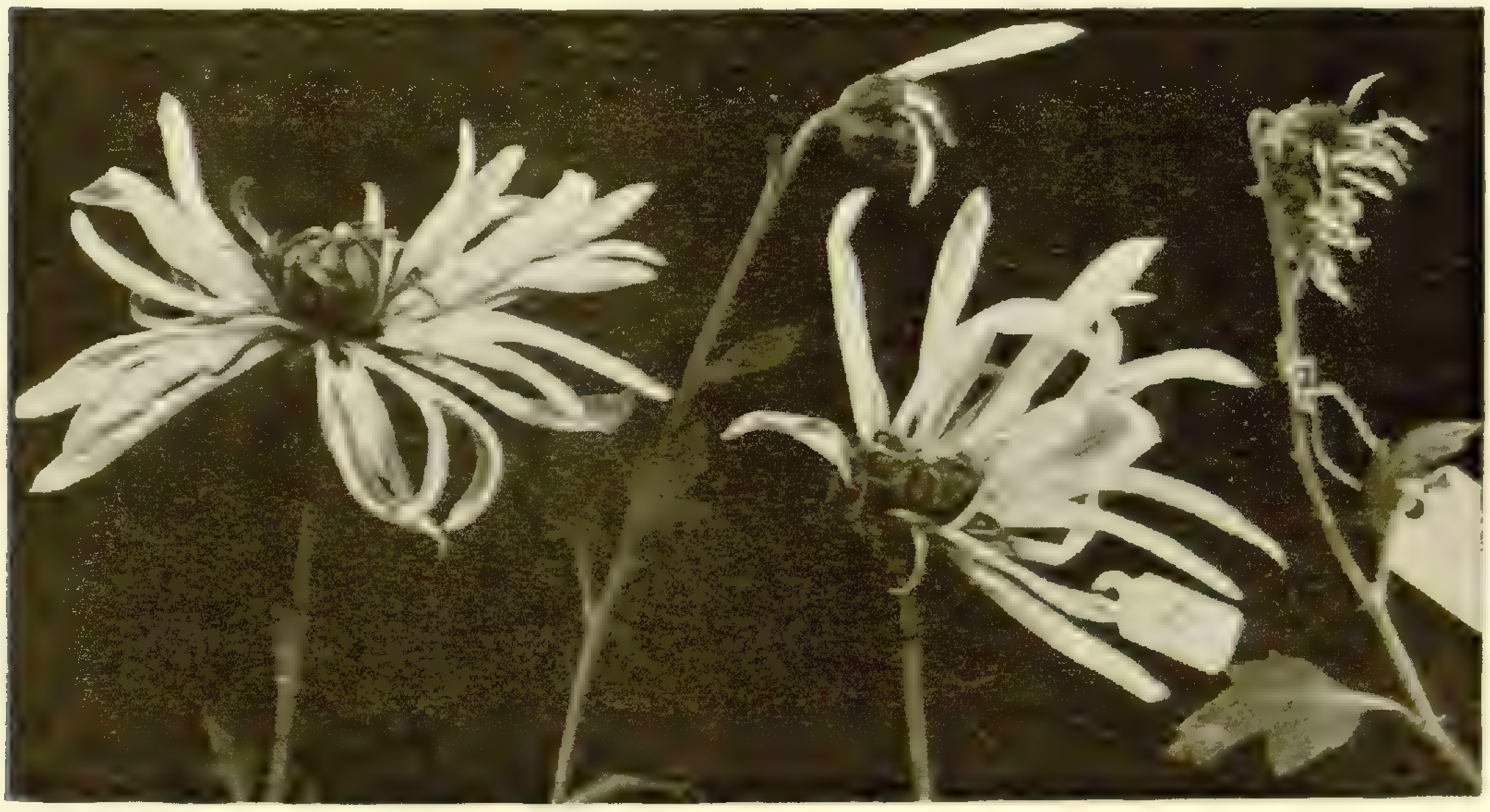

FIG. 13.—Four diseased heads produced by inoculation from pure culture.

Inoculation no. 4: control cultures similar to no. 3 with sterile needle; examined December 8 and 18, no growth.

Inoculation no. 5: at base of leaf; the tissue unbroken; examined December 8 and 18, no result.

Inoculations nos. 6, 8: agar laid upon the outside of the involucre; tissue uninjured; examined December 8 and 18, no results.

Inoculation no. 7: lost through accident.

Inoculation no. 9: at the base of the petiole; tissue uninjured; examined December 8 and 18, no result.

Inoculation no. 10: leaf base pricked and inoculated with agar culture; examined December 8 and 18, no results.

It is to be noted that in this series nos. 1 and 3 produced typical disease; that is, all of the inoculations which were attempted within the involucre. Control inoculations produced no growth, and attempts to produce the disease upon leaves and stems through uninjured tissue failed.

Series II

Inoculated November 24, 1906, with mycelium which was richly set with pycnidia.

Inoculations nos. 11, 12: agar bearing mycelium placed deep between the petals of the open flower; examined December 8, showed typical disease.

Inoculation no. 13: same as no. 11 using sterile agar; control inoculation; examined December 8 and 18, no growth.

Inoculation no. 14: peduncle immediately below the bud scarified and inoculated with mycelium on agar; examined December 8, typical disease.

Inoculation no. 15: similar to no. 14, but with sterile agar; control experiment; examined December 8 and 18, no growth.

Inoculation no. 16: upon scarified stem immediately under head with agar bearing mycelium, the whole covered with wet cotton; examined December 8 and 18, no result.

Inoculation no. 17: conditions same as in no. 16; examined December 18, head typically diseased.

Inoculation no. 18: conditions same as in no. 16; examined December 8, no result; December 10, typical disease.

Inoculation no. 19: agar bearing mycelium placed upon the tip of the opening head; examined December 8, no growth; December 18, typical disease.

Inoculation no. 20: conditions same as in no. 19; examined December 8, typical disease.

Inoculation no. 21: conditions same as in no. 19; lost through accident.

It is to be observed that in this series the inoculations within the flower produced typical disease. Control inoculations produced no disease. Inoculation upon scarified stem when covered with damp cotton to prevent evaporation was capable of inducing the disease.

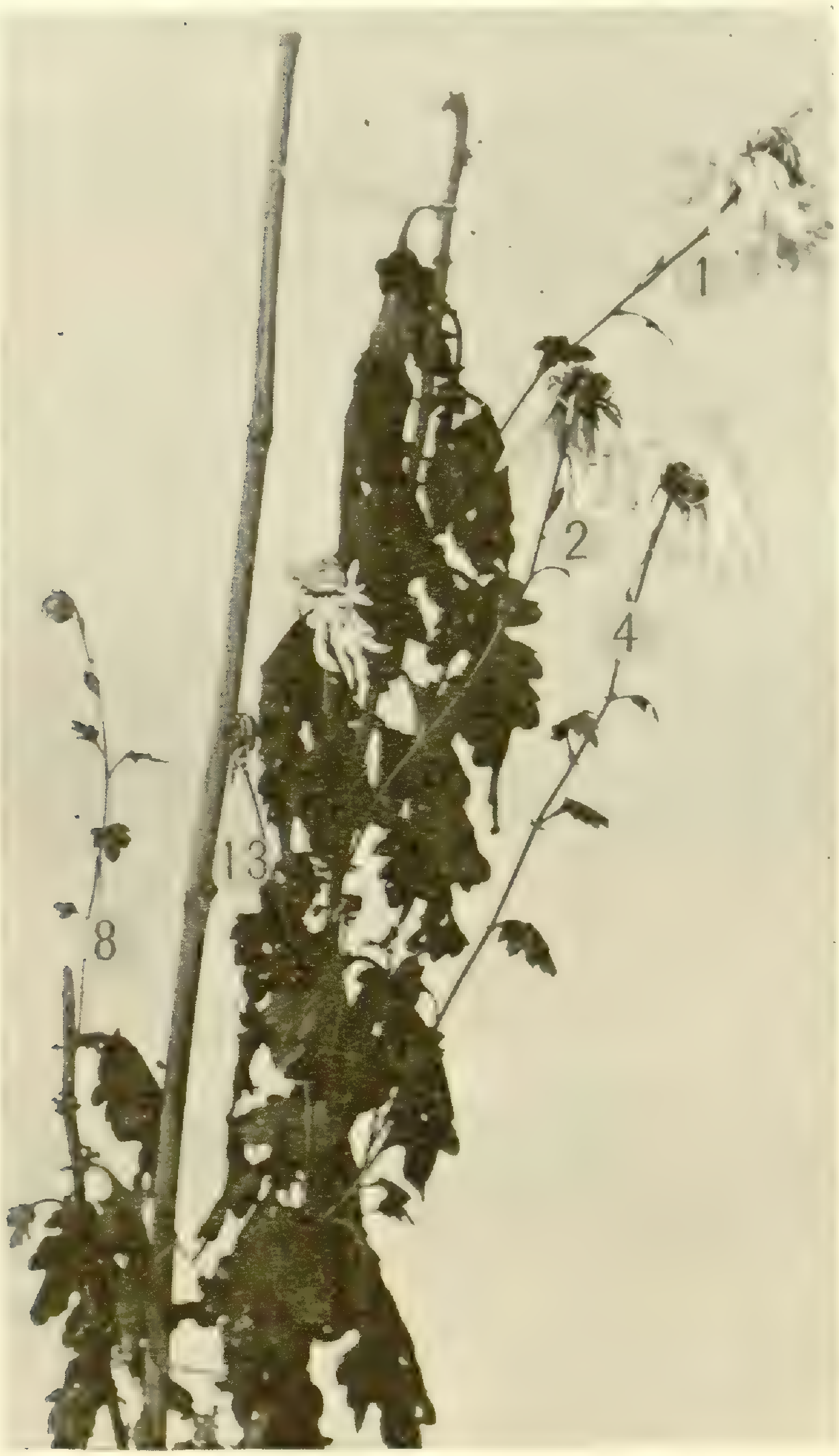

FIG. 14

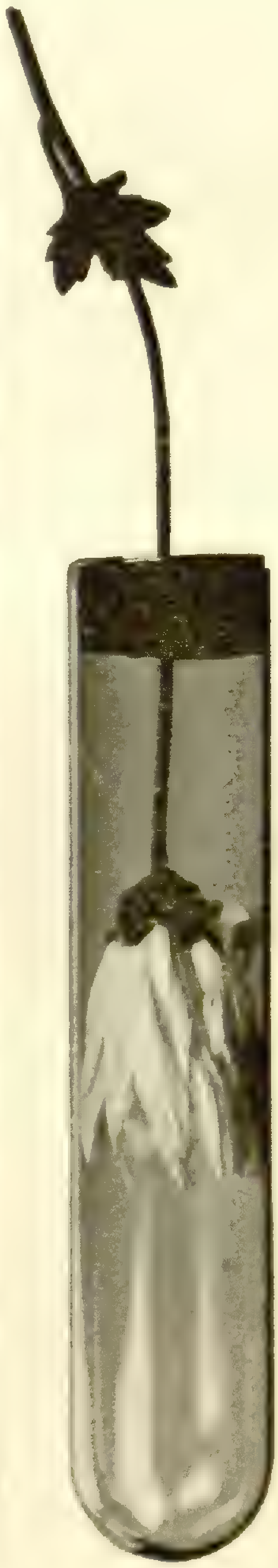

FIG. 15

FIG. 14. Plant bearing flowers in condition of disease; produced by inoculation. *1*, The topmost head inoculated between the flowers with pycnidia from agar. *2*, The second tallest head as in no. 1. *4*, Inoculated on scarified bark immediately below the head. Dates as above. *13*, Inoculated no. 29 inside involucre, covered by tube 24 hours; diseased December 8. *8*, Inoculated November 24 with agar on scarified bark under wet cotton; diseased December 10.—FIG. 15. Showing method of covering inoculated heads to supply humid atmosphere.

Series III

Inoculated November 29, 1906.

Inoculation no. 22: agar bearing mycelium was placed between the rays of a head and the whole covered with a tube and supplied with wet cotton to prevent evaporation; tube and cotton removed next day; examined December 8, typical disease.

Inoculation no. 23: similar to no. 22 but inoculation made just inside the involucre; examined December 8, typical disease.

Inoculation no. 24: similar to no. 22 but upon the tip of the bud; covering tube removed after two days; examined December 8, typical disease.

Inoculation no. 25: a single ray from a diseased flower placed among the rays of a flower just beginning to open, which were left uncovered; examined December 8, typical disease.

Inoculation no. 26: similar to no. 25; but covered with tube as in no. 22; examined December 8, typical disease.

Inoculation no. 27: similar to no. 22; examined December 8, typical disease.

From inoculations nos. 22, 23, 24, and 27 it seems evident the protection of the inoculations from evaporation for 24 or 48 hours leads to greater certainty and rapidity of infection. Inoculations nos. 25 and 26 go to show the lack of necessity for any covering when diseased rays are used with which to inoculate. It is possible that the mycelium is in a more vigorous condition in such diseased rays.

Series IV

Inoculations made November 30, 1906, from very vigorously growing mycelium from a plate of cow pea agar.

Inoculations 28 to 31: made from the extreme tip of the mycelium taken from the edge of the colony; inoculation under the outer rays; examined December 8, no growth; December 18, typical disease in all.

Inoculations 32 to 35: inoculating material taken from the youngest dense zone in the colony; inoculated as in nos. 28 to 31; examined December 8, no growth; December 18, all typically diseased.

Inoculations 36 to 40: inoculating material taken from the center of the colony, the agar being full of old, dark, thick hyphae; examined December 8, all showed typical cases of disease.

It seems apparent from this series that the mycelium from the older central portions is capable of producing quicker infection than that from the outer region of the colony.

RECOVERY OF FUNGUS FROM INOCULATED HEADS

In many cases rays were taken from the heads which were made diseased by inoculation and these rays were thrown upon Petri dishes containing solidified pea agar, with the result that in each case the petal was soon the center of the pure colony of a fungus identical with that used in the inoculation.

As a result of all of these inoculations it seems clear that the fungus in question is actually the cause of the diseased condition of the blossom; that it can gain entrance to the tissue of the blossom much more easily than to the tissue of the leaves, petioles, and stems; and that humidity at the time of inoculation favors the success of the inoculation.

I desire to acknowledge my indebtedness to Mr. J. G. Hall, Assistant Pathologist, for the illustrations accompanying this article.

MEDIA USED

Cow pea agar: 500 grams of fresh cow pea pods and contents were stewed in one liter of water for one half-hour, drained, 1 per cent. agar added, autoclaved at 110°, and filtered.

Cow pea leaf agar: 500 grams of cow pea leaves and petioles were stewed in one liter of water for one half-hour, drained, 1 per cent. agar added, autoclaved at 110°, and filtered.

Pea agar: ten garden peas were autoclaved with 1 liter of water for one-half hour, drained, 1 per cent. agar added, autoclaved at 110°, and filtered.

Four per cent. pea agar: four per cent. by weight of dry peas were stewed with 1 liter of water for one-half hour, drained, 1 per cent. agar added, autoclaved at 110°, and filtered.

Standard beef agar: according to the rules of the American Public Health Association.

Standard beef gelatin: according to the rules of the American Public Health Association.

Pure agar: 1 per cent. agar without addition of nutrients.

Litmus lactose agar: standard beef agar with the addition of 1 per cent. lactose, and litmus sufficient to color.

Lettuce agar: 10 grams of lettuce leaves and petioles were stewed in water for one half-hour, drained, 1 per cent. agar added, autoclaved at 110°, and filtered.

Boiled rice: 2 grams of washed rice to 8^{cc} of water, tubed, autoclaved at 110°.

Boiled corn: 2 grams of washed corn to 8^{cc} of water, tubed, autoclaved at 110°.

Glucose agar and *starch agar:* made by adding percentages indicated to pure agar, and sterilizing intermittently.

Peptone agar: made by adding per cent. indicated to pure agar and autoclaving at 110°.

WEST RALEIGH, N. C.

ON THE IMPORTANCE OF PHYSIOLOGICALLY BALANCED SOLUTIONS FOR PLANTS

II. FRESH-WATER AND TERRESTRIAL PLANTS

W. J. V. OSTERHOUT

(WITH SEVEN FIGURES)

If the facts set forth in the first part[1] of this paper prove to be valid, not for marine plants only, but also for all other kinds, we cannot suppose them to be merely the result of adaptation to a particular environment, but must consider them to be the direct expression of certain fundamental characteristics of living matter. In order that the evidence on this important point might be as complete as possible, a wide range of material was studied. It includes both lower and higher algae, liverworts, Equisetaceae, and several species of flowering plants, embracing among the latter both fresh-water aquatics and land plants. The solutions were made up with all the precautions regarding distilled water and purity of salts described in the first part of this paper. The solutions had the same compositions as there described, except that lower concentrations were employed. A control series was always made, in which all solutions were made faintly alkaline. The material was always rinsed in distilled water before being placed in the solutions. The plants were in all cases exposed to fairly bright light, but not to direct sunlight. The temperature averaged between 18° and 20°C., and was not subject to much fluctuation.

ALGAE

The most extensive series of experiments on algae was made with Vaucheria and Spirogyra. A form of *Vaucheria sessilis*, abundant in running water, was chosen because it readily gives off zoospores when brought into the laboratory. Tufts of this material, washed free from all adhering dirt, were placed in glass dishes and covered with tap water. Glass slides were placed upright in the dishes. On the following morning numerous zoospores were found attached to each slide at the water level. As many as fifty to a hundred zoospores were commonly found arranged in a row across the slide, so that subsequent observation was an easy matter. The slides were thoroughly rinsed in distilled water and transferred to the solutions. The solutions were contained in glass tumblers, in which the slides were placed in an upright position, care being taken to have the zoospores always at the same depth below the surface. The volume of the solution, 100^{cc}, was very large compared with that of the zoospores. The tumblers were covered with glass plates to exclude dust and hinder evaporation. Under these circumstances the plants thrive excellently and in favorable solutions produce normal mature fruit.[2]

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[1] BOTANICAL GAZETTE 42:127–134. 1906.

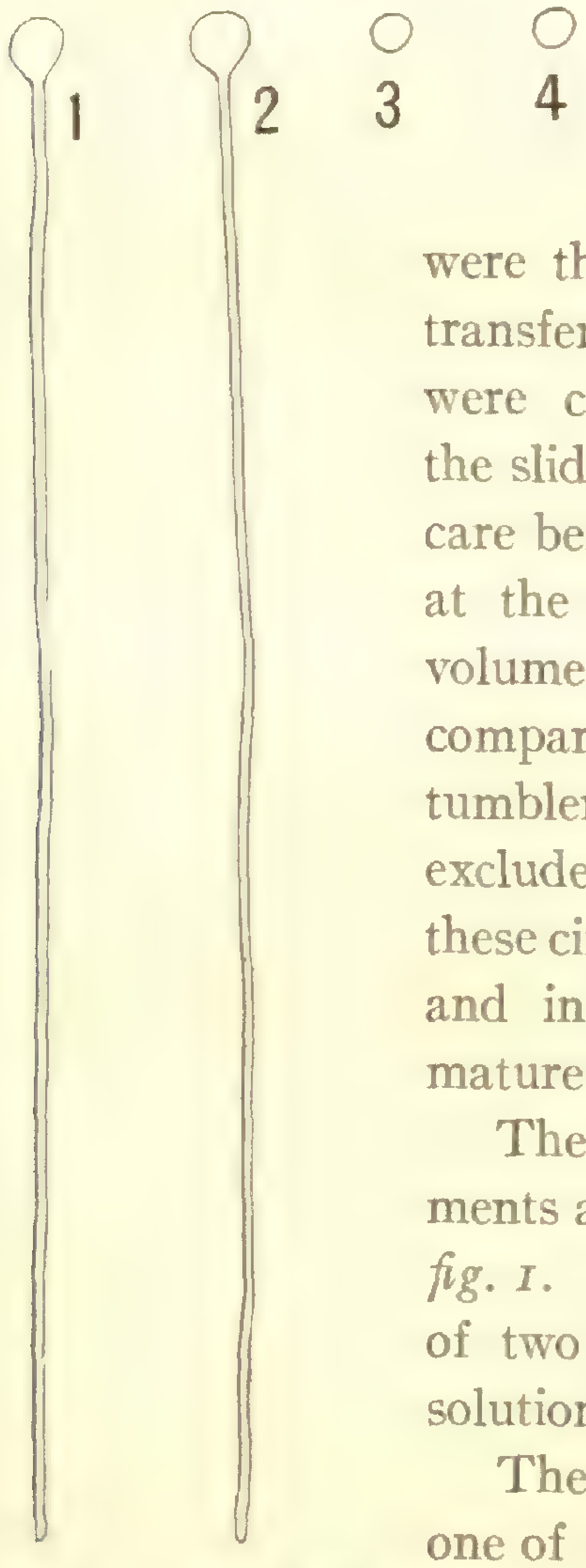

FIG. 1.—Growth of zoospores of Vaucheria during 25 days in various $m/100$ solutions. The quantities are stated in cubic centimeters, the length in millimeters, and the gain in length in per cent. **1**, distilled water, length 9.4, gain 5000. **2**, NaCl 1000 + $CaCl_2$ 10, length 9.4, gain 5000. **3**, NaCl, length 0.18, gain 0. **4**, $CaCl_2$, length 0.18, gain 0.

The average results of six series of experiments are given in Table III and illustrated in *fig. 1*. The figure shows clearly how a mixture of two poisonous substances may produce a solution as harmless as distilled water.

The species of Spirogyra employed is a large one of the *majuscula* type. The material was transferred from the pond directly to distilled water; after being rinsed in this it was placed in covered glass dishes containing each 200^{cc} of solution.

It will be seen that these results agree in the most striking way with those already described for marine plants.

Further experiments were made with a variety of other algae, including a species of blue-green alga (Oscillatoria), Chlamydomonas, Closterium and two other species of desmids, a diatom (Navicula), and a species of Oedogonium. The results agree closely with those given below. There can be little doubt, therefore, that the algae in general, both fresh-water and marine, obey the same law.

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[2] *Cf.* OSTERHOUT, Extreme toxicity of sodium chloride and its prevention by other salts. Jour. Biol. Chemistry **1**:363. 1906.

TABLE III. ALGAE

A plus sign indicates that the plants were alive when the experiment was stopped. All quantities given are cubic centimeters of $3m/32$ solutions.

Culture Solution	Duration of Life in Days	
	Vaucheria	Spirogyra
Dilute sea water (total salts 0.6 per cent.)	40+	95+
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	40+	95+
Distilled water	40+	95+
Tap water	40+	95+
NaCl	$\frac{1}{100}$	$\frac{3}{4}$
1000 NaCl 10 $CaCl_2$	21	60
1000 NaCl 22 KCl 10 $CaCl_2$	40+	65
1000 NaCl 78 $MgCl_2$ 10 $CaCl_2$	40+	65
1000 NaCl 78 $MgCl_2$ 22 KCl	$\frac{2}{3}$	2
1000 NaCl 22 KCl	$\frac{1}{5}$	2
1000 NaCl 78 $MgCl_2$	$\frac{2}{3}$	$1\frac{3}{4}$
1000 Dist. H_2O 78 $MgCl_2$ $= m/147$ $MgCl_2$	$1\frac{1}{2}$	2
1000 Dist. H_2O 22 KCl $= m/495$ KCl	$2\frac{1}{2}$	3
1000 Dist. H_2O 10 $CaCl_2$ $= m/1077$ $CaCl_2$	9	95+

LIVERWORTS

The gemmae of Lunularia furnish ideal material for studies on the effects of solutions. They can be obtained at any time of year, they grow readily when floating on the surfaces of solutions, and are fairly uniform in behavior. The material used in these experiments was obtained in part from a greenhouse and in part from moist banks of earth along streams. Material from different sources was never mixed together in any series of experiments.

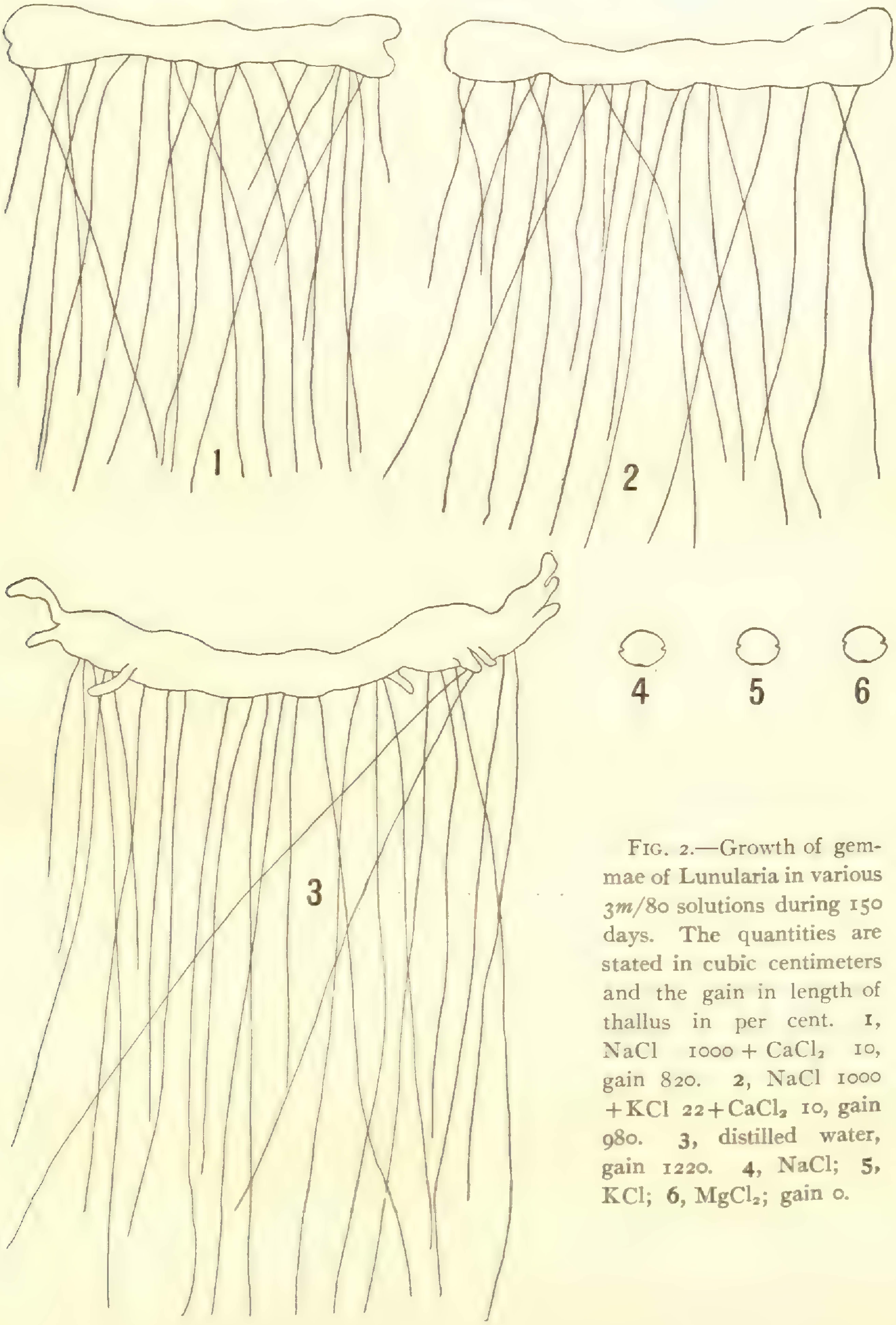

FIG. 2.—Growth of gemmae of Lunularia in various $3m/80$ solutions during 150 days. The quantities are stated in cubic centimeters and the gain in length of thallus in per cent. **1**, NaCl 1000 + $CaCl_2$ 10, gain 820. **2**, NaCl 1000 + KCl 22 + $CaCl_2$ 10, gain 980. **3**, distilled water, gain 1220. **4**, NaCl; **5**, KCl; **6**, $MgCl_2$; gain 0.

The gemmae were removed from the cups with the point of a knife and sprinkled on the surface of the solution, care being taken to exclude particles of dust and dirt. Each tumbler contained 200^{cc} of solution and was covered with a glass plate. The gemmae may be easily removed from the surface of the solution for purposes of observation by dipping into it a clean slide and slowly raising it at an angle so as to take up the material upon one side only. The material should not be replaced in the solution unless extreme care be taken to prevent contamination.

The average results of six series of experiments are given in Tables IV and V, and illustrated in *figs. 2* and *3*.

TABLE IV. LUNULARIA

A plus sign indicates that the plants were alive when the experiment was stopped. All quantities given are cubic centimeters of $3m/32$ solutions.

Culture Solution	Duration of Life in Days
Dilute sea water; total salts 0.6 per cent	200+
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	200+
Distilled water	200+
NaCl	4
1000 NaCl 10 $CaCl_2$	100
1000 NaCl 22 KCl 10 $CaCl_2$	200+
1000 NaCl 78 $MgCl_2$ 10 $CaCl_2$	200+
1000 NaCl 78 $MgCl_2$ 22 KCl	9
1000 NaCl 22 KCl	4
1000 NaCl 78 $MgCl_2$	7
$MgCl_2$	2
KCl	12
$CaCl_2$	100

TABLE V. LUNULARIA

All quantities given are cubic centimeters of $3m/80$ solutions

CULTURE SOLUTION	GROWTH IN 150 DAYS		
	Length of thallus in mm.	Per cent. increase in length of thallus	Aggregate length of rhizoids per thallus in mm.
Dilute artificial sea water: 1000 Nacl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	6.52	1204	168
Distilled water	6.60	1220	180
NaCl	0.50	0	0
1000 NaCl 10 $CaCl_2$	4.60	820	114
1000 NaCl 22 KCl 10 $CaCl_2$	5.40	980	123.5
1000 NaCl 78 $MgCl_2$ 10 $CaCl_2$	5.50	1000	125
1000 NaCl 78 $MgCl_2$ 22 KCl	0.54	8	0.3
1000 NaCl 22 KCl	0.50	0	0
1000 NaCl 78 $MgCl_2$	0.52	4	0.1
$MgCl_2$	0.50	0	0
KCl	0.50	0	0
$CaCl_2$	4.55	810	90

EQUISETUM

The spores of Equisetum retain their vitality for only a few days. The fruiting cones were brought into the laboratory and allowed to stand for a day or two. The freshly shed spores were then placed on the surfaces of solutions in covered glass dishes. They germinate rapidly and in a few days produce prothallia of fair size. The average results of four series of experiments are shown in Table VI and *fig. 4*.

FLOWERING PLANTS

The most extensive series of experiments was made with wheat. The variety selected is known as Early Genesee. The percentage of germination is very high and the growth is vigorous from the start. The plan first tried was that of carefully placing the seeds on the surface of the solutions so that they float. This worked well with

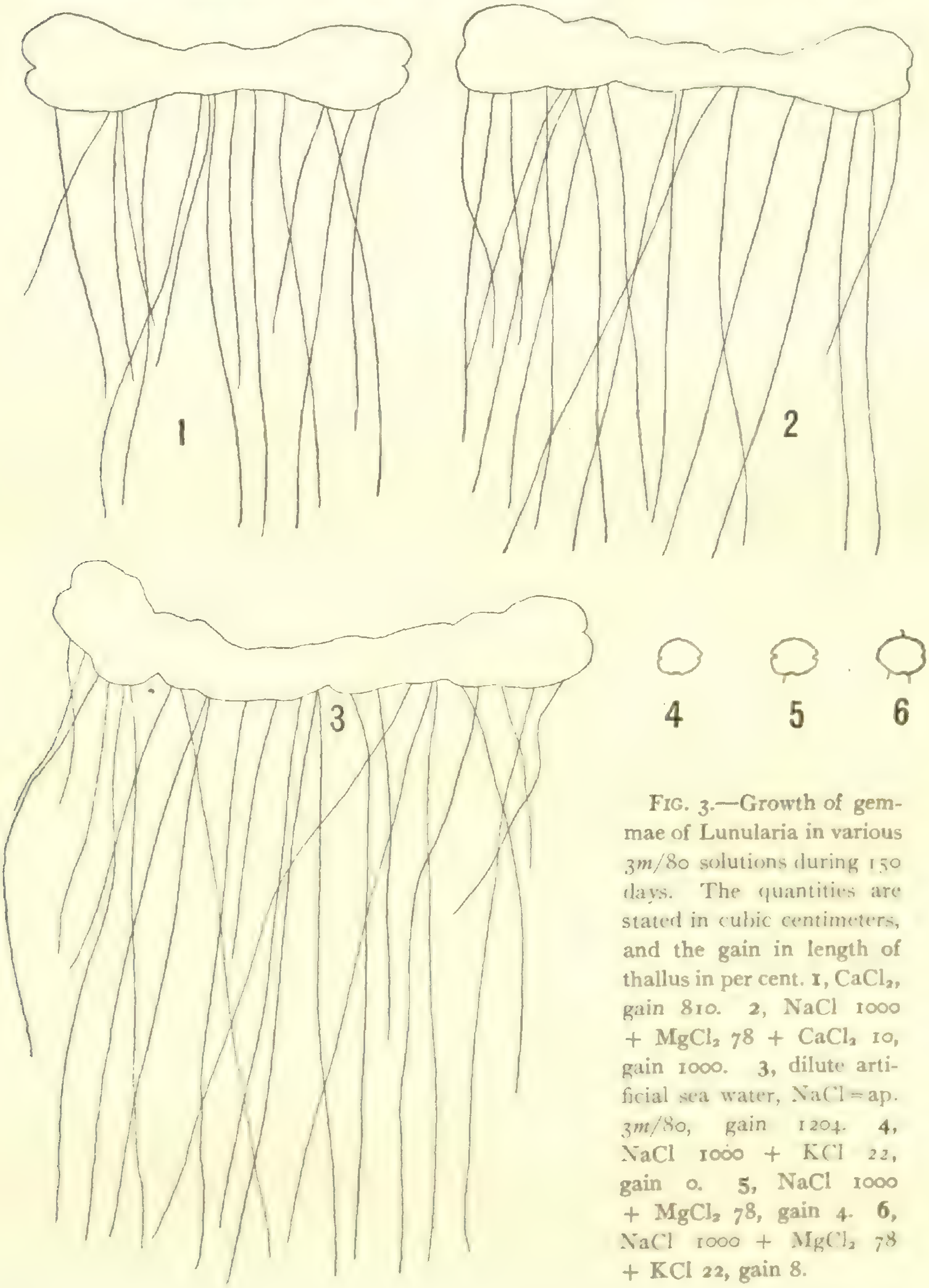

FIG. 3.—Growth of gemmae of Lunularia in various $3m/80$ solutions during 150 days. The quantities are stated in cubic centimeters, and the gain in length of thallus in per cent. **1**, $CaCl_2$, gain 810. **2**, NaCl 1000 + $MgCl_2$ 78 + $CaCl_2$ 10, gain 1000. **3**, dilute artificial sea water, NaCl = ap. $3m/80$, gain 1204. **4**, NaCl 1000 + KCl 22, gain 0. **5**, NaCl 1000 + $MgCl_2$ 78, gain 4. **6**, NaCl 1000 + $MgCl_2$ 78 + KCl 22, gain 8.

wheat and other small seeds during the first stages of germination; but if the experiments are to be carried beyond this stage, the seedlings must be supported so that the leaves do not come into contact with the solution. After some trials the following device was hit upon which answers the purpose admirably. A strip of filter paper is folded lengthwise and one of the folds turned back as shown in *fig. 5*. The seeds are placed in the trough thus formed and the whole strip is then bent into a circle and placed in a tumbler previously filled with solution. The strip should be of such length that when placed in the top of the tumbler the ends just meet and so form a stiff collar which just fits inside the top of the tumblers and which will not slip down. A large number of these collars may be prepared, filled with seeds, bent into circles, and secured by ordinary paper-clips placed on the overlapping ends. They may be piled in trays until wanted. It is then only necessary to remove the clips and set the collars in glasses previously filled with solutions.

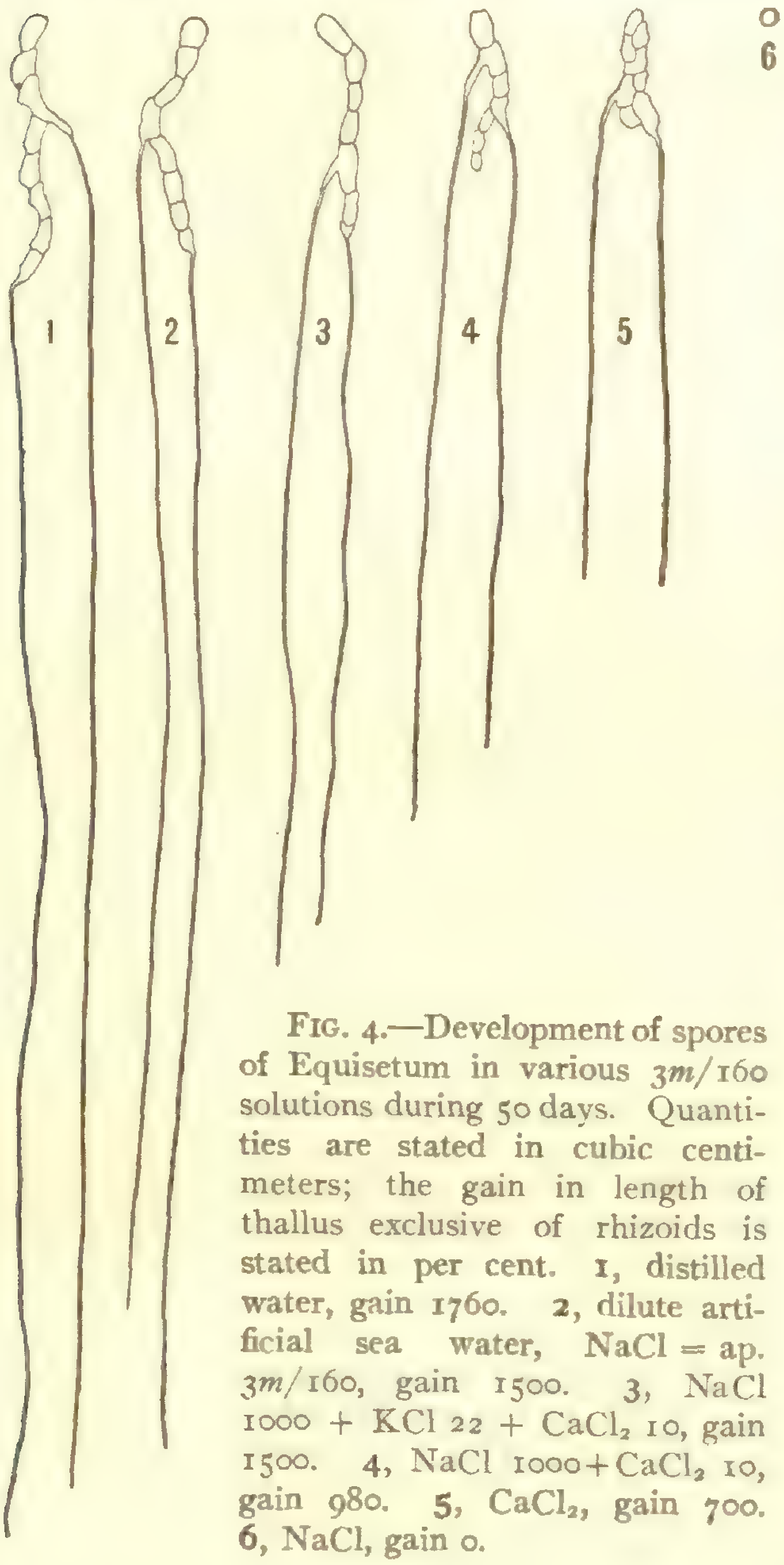

FIG. 4.—Development of spores of Equisetum in various $3m/160$ solutions during 50 days. Quantities are stated in cubic centimeters; the gain in length of thallus exclusive of rhizoids is stated in per cent. 1, distilled water, gain 1760. 2, dilute artificial sea water, $NaCl$ = ap. $3m/160$, gain 1500. 3, $NaCl$ 1000 + KCl 22 + $CaCl_2$ 10, gain 1500. 4, $NaCl$ 1000 + $CaCl_2$ 10, gain 980. 5, $CaCl_2$, gain 700. 6, $NaCl$, gain 0.

In some cases, especially where larger glasses are employed, a strip of paper of double thickness may be used; this makes a stiffer collar. It is then advisable to perforate the bottom of the seed trough by means of a tracing wheel such as is used for patterns. This allows the roots to penetrate the paper freely and without delay.

Care should be taken that the solution does not cover the seeds. The paper must be spread open at the top so as to allow the air to come into direct contact with the seeds. The micropyle should be in contact with the moist filter paper.

Careful experiments were made to determine whether the filter paper exerted any influence on the solution (by absorption, etc., or by concentration of the solution about the seed as the result of evaporation) which might affect the results, but no such influence

TABLE VI. EQUISETUM

All quantities given are cubic centimeters of $3m/160$ solutions.

Culture Solution	Growth in 50 Days		
	Length of thallus in mm.	Per cent. increase in length of thallus, exclusive of rhizoids	Aggregate length of rhizoids per thallus in mm.
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	0.80	1500	8.1
Distilled water	0.93	1760	9.0
NaCl	0.05	0	0
1000 NaCl 10 $CaCl_2$	0.54	980	4.7
1000 NaCl 22 KCl 10 $CaCl_2$	0.80	1500	5.2
1000 NaCl 78 $MgCl_2$ 10 $CaCl_2$	0.93	1760	9.0
1000 NaCl 78 $MgCl_2$ 22 KCl	0.07	40	0
1000 NaCl 22 KCl	0.05	0	0
1000 NaCl 78 $MgCl_2$	0.07	40	0
$MgCl_2$	0.05	0	0
KCl	0.05	0	0
$CaCl_2$	0.40	700	3.2

could be detected. The solutions were renewed from time to time and the concentration ascertained by occasional titration.

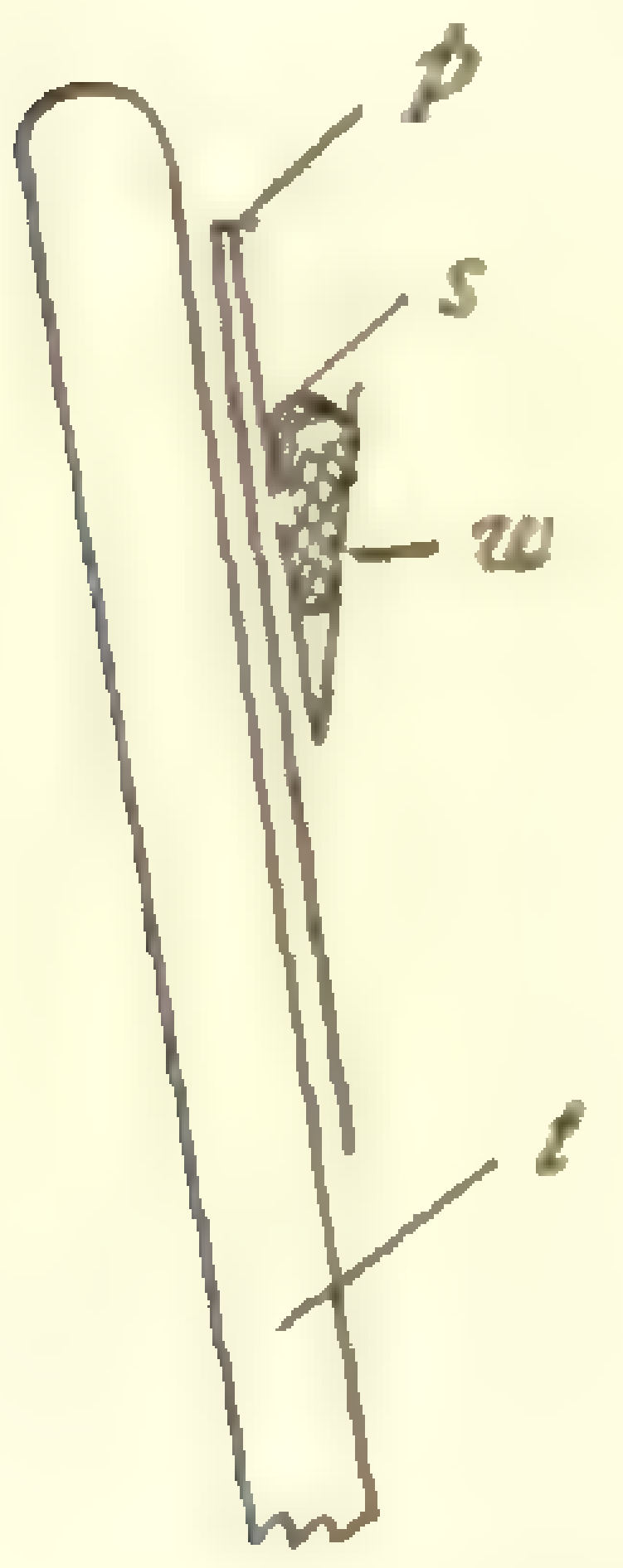

FIG. 5.—Sectional view of wall of tumbler and seed supported by folded filter paper; *p*, paper; *s*, seed; *t*, tumbler; *w*, water line.

It should be said that in general the growth of roots (or any parts in direct contact with the solution) furnishes a much better criterion of the effect of solutions than the aerial portions of the plant. In certain solutions which are so poisonous that the roots cannot develop, the leaves may grow fairly well for a time. In these cases the poisonous solutes are apparently filtered out by the tissues of the seed as the solution passes through them on its way to the leaf. For this reason the figures for the growth of roots only are here given. The results are shown in Table VII and *figs. 6* and *7*, which give the average of five series of experiments. Each number represents average measurements of at least four or five hundred seeds. This is necessary in order to do away with the individual variation so common in seeds.

TABLE VII. WHEAT

All quantities given are cubic centimeters of $3m/25$ solutions.

CULTURE SOLUTION	GROWTH IN 40 DAYS Aggregate length of roots per plant in mm.
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	360
Distilled water	740
NaCl	59
1000 NaCl 10 $CaCl_2$	254
1000 NaCl 22 KCl 10 $CaCl_2$	324
1000 NaCl 78 $MgCl_2$ 10 $CaCl_2$	327
$MgCl_2$	7
KCl	68
$CaCl_2$	70

A similar though less extensive series of experiments was carried out with flax, alfalfa, red-beet, and radish seeds. Another series was made by placing pieces of the fresh-water aquatics, Zannichellia and Potamogeton, in solutions, or in the case of Lemna, by allowing the plants to float on the surface. The results in all these cases were similar to those given above.

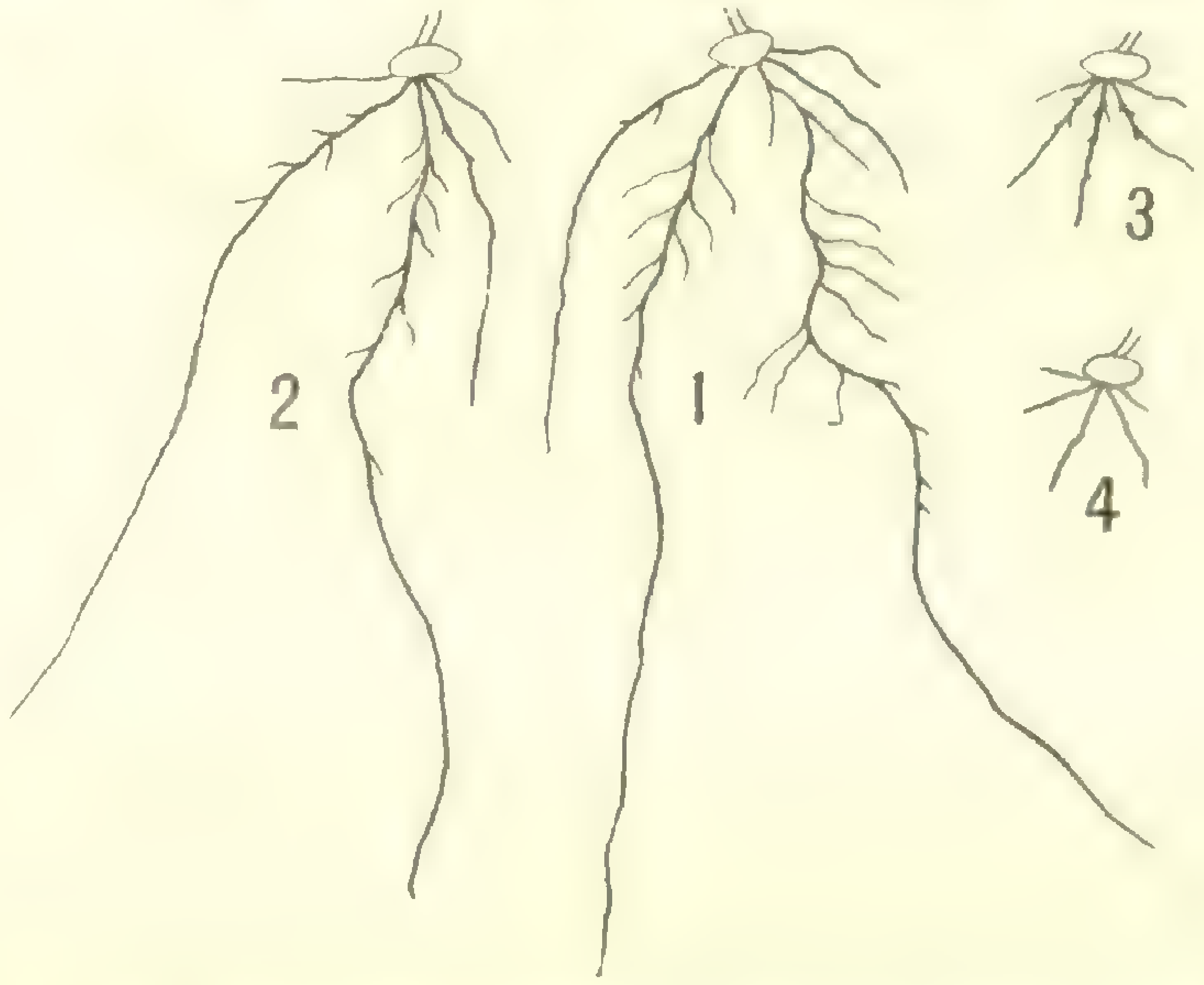

FIG. 6.—Growth of roots of wheat in various $3m/25$ solutions. Quantities are stated in cubic centimeters, and the aggregate length of roots in millimeters. 1, NaCl 1000 + KCl 22 + $CaCl_2$ 10, length 324. 2, NaCl 1000 + $CaCl_2$ 10, length 254. 3, $CaCl_2$, length 70. 4, NaCl, length 59.

It is thought desirable to see how cuttings would behave under similar treatment. Cuttings (about nine inches in length) of Tradescantia and Tropaeolum were placed upright in bottles, the lower three inches of the plant being submerged

TABLE VIII. CUTTINGS

All quantities given are cubic centimeters of $3m/32$ solutions.

CULTURE SOLUTION	GROWTH IN 10 DAYS	
	Tradescantia	Tropaeolum
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	Long roots	Long roots
Distilled water	Very long roots	Very long roots
NaCl	No roots	No roots
1000 NaCl 10 $CaCl_2$	Short roots	Short roots
1000 NaCl 22 KCl 10 $CaCl_2$	Medium length roots	Medium length roots

in the solution. Absorbent cotton was packed in the neck of the bottle to exclude dirt and hinder evaporation. The results were similar to those described above, as will be seen from Table VIII.

Finally the question was raised whether the tissues of the stem and leaf, if brought into direct contact with the solution, would behave like the root. To answer this, sections of considerable (but uniform) thickness were cut with a microtome and placed in the solutions. The results appear in Table IX.

The results described in this paper are in all essentials in striking agreement with those obtained from the study of marine plants, as well as from the study of marine and fresh-water animals as referred to in the first part of this paper. This agreement shows that the principle of balanced solutions is of general validity.[3] The application of this principle to soil and river water[4] and to nutrient solutions, I hope to take up in a subsequent paper.

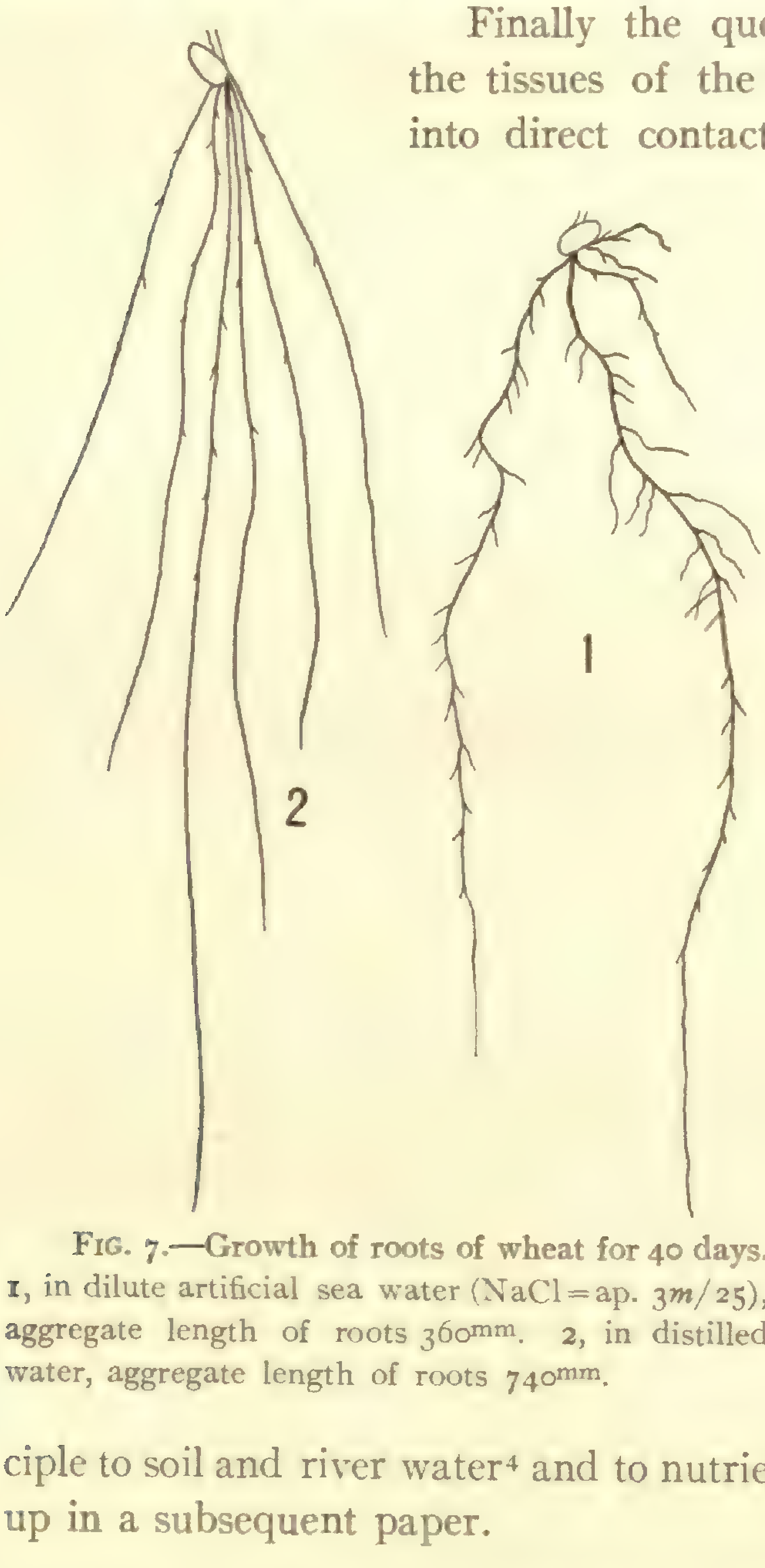

FIG. 7.—Growth of roots of wheat for 40 days. 1, in dilute artificial sea water (NaCl = ap. $3m/25$), aggregate length of roots 360mm. 2, in distilled water, aggregate length of roots 740mm.

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[3] LOEW and his pupils have shown that calcium antagonizes magnesium (cf. Bull. No. 18, Div. Veg. Phys. and Path. U. S. Dept. Agric. 1899). See also the antagonistic effects noted by KEARNEY and CAMERON (Report No. 71, U. S. Dept. Agric. 1902) in their studies on the salts of alkali soils. The method employed by them (observation of the root-tip only) is so different from mine that I have not attempted to compare the results.

[4] In the first part of this paper I have referred to the composition of tap water, but it seems advisable to defer the discussion of this point.

TABLE IX. SECTIONS

All quantities given are cubic centimeters of $3m/32$ solutions.

Culture Solution	Duration of Life in Days			
	Red beet: Cross-sections of root	Mesembryanthemum: Cross-sections of leaf	Tradescantia: Cross-sections of stem	Tropaeolum: Cross-sections of leaf
Dilute artificial sea water: 1000 NaCl 78 $MgCl_2$ 38 $MgSO_4$ 22 KCl 10 $CaCl_2$	35	16	19	25
Distilled water	35	18	20	32
NaCl	18	9	12	14
1000 NaCl 10 $CaCl_2$	25	12	18	20
1000 NaCl 22 KCl 10 $CaCl_2$	30	15	19	22

For the sake of clearness it seems desirable to call attention to the distinction between balanced solutions and ordinary nutrient solutions. A nutrient solution may be used in such dilute form that none of its components could exert any toxic action even if the other constituents were removed. In this case there are no poisonous effects to be inhibited and consequently no balancing of the solution is required. Our only concern is to supply all the substances needed for nutrition, irrespective of any balancing action, and so form a *complete* nutrient solution.

If we increase the concentration of this solution, however, we soon reach the point where some or all of the components begin to exert their individual toxic effects, whereupon it may become necessary to inhibit these effects by proper adjustment of the relative proportions of the substances present or by the addition of other substances. The substances added to produce a balance do not necessarily have a nutritive value. For example, LOEB[5] was able to balance certain solutions by adding zinc, cobalt, aluminum, etc.[6]

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[5] Am. Jour. Physiology 6:411–433. 1902.

[6] To make clear this distinction between balanced and nutrient solutions is more necessary, since LOEW and ASO (Bull. Coll. Agr. Tokyo Imp. University 7:395. 1907) confuse the two kinds of solutions. Their criticisms are wholly based on this misconception and do not affect the matter as I have presented it. The distinction between nutrient and balanced solutions is due to LOEB, who has explained it clearly in his *Dynamik der Lebenserscheinungen* 115–120.

In general we may know when the solution is properly balanced by comparing its effects with those of *pure*[7] distilled water. In a properly balanced solution we expect the organism to live approximately as long as in distilled water, and while it will not grow so fast (on account of the osmotic pressure), the ultimate development reached should be comparable with that attained in distilled water.[8]

Why all these effects are so, we are not at present prepared to say in detail. LOEB has gone farther than any other in the explanation of these phenomena, referring them to the effects of salts and ions on proteids[9]. According to his conception any metal must be poisonous when it alone is present in the solution, for it will enter the proteids and drive out other metals in accordance with the law of mass action. This will of course alter the properties of the proteids and so cause disturbances in function. The only way to prevent this is to maintain a proper balance between the various metals in the solution. It may be pointed out that an analogy exists between the effects described here and various reactions in which proteids are involved. Antagonism between Na and Ca, for example, is see in the clotting of blood, which is hindered by Na and favored by Ca.

The thing of chief importance is the agreement in behavior of such a great diversity of plants with the fresh-water and marine animals already studied. Thereby is brought to light a new point of similarity between animals and plants which is fundamental in character and which must be taken into consideration in attempting to formulate a theory of living matter.

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[7] Water twice distilled from glass, the first third of the distillate being rejected, is usually regarded as pure. But such water may be quite poisonous if any part of the apparatus, including stoppers, be new. The longer the apparatus is used the less poisonous the water becomes, until it finally ceases to be toxic.

[8] Higher concentrations excepted.

[9] See references in the first part of this paper, BOT. GAZ. **42**: 134. 1906

FERTILIZATION AND EMBRYOGENY IN EPHEDRA TRIFURCA[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 102

W. J. G. LAND

(WITH PLATES XX–XXII)

Little attention has been given to the fertilization and embryogeny of Ephedra, the only accounts being those of STRASBURGER and JACCARD. In 1872 STRASBURGER,[2] studying *E. altissima*, described and figured unfertilized eggs and four stages of the embryo immediately before and after formation of cotyledons. In 1876 he described[3] a series of stages in *E. altissima* from the central cell of the archegonium to the formation of suspensors. He noted the penetration of the pollen tube, which, he says, reaches the egg through a canal formed by the breaking-down of the neck cells of the archegonium. Fertilization was not observed, but several stages of the proembryo were noted. Usually three to eight proembryos are formed and arranged in a row down the middle of the egg. He calls attention to what he considers an abnormal condition, in which the cytoplasm of the egg is pierced through by irregular tortuous channels supported throughout their length by kinoplasmic fibers. These channels extend around and finally inclose a portion of the egg cytoplasm together with a single nucleus. He thinks these channels result from the activities of this single nucleus which is finally inclosed. The breaking-out of the suspensors from the archegonia was noted. His third account,[4] published in 1879, deals at some length with the embryogeny of *E. campylopoda*, but adds little to the results obtained from *E. altissima*.

In 1894 JACCARD,[5] studying *E. helvetica*, observed the pollen tube entering the archegonium, one male nucleus in contact with the egg nucleus, and the second male nucleus, the stalk cell, and the tube nucleus lying in the micropylar end of the egg. He also studied pollen tubes grown in five per cent. gelatin in sterilized pear juice. He noted the disorganization of the jacket cells and describes a fusion of the nuclei of the jacket cells with one another and their subsequent migration into the cytoplasm of the egg. He also observed a large number of small nuclei in the egg, the nature and origin of which he was not able to determine. He further states that a suspensor ("prosuspenseur" or "embryonalschlauch") is not formed. The elongation of the basal cells of the embryo to form a secondary suspensor ("le columelle") is noted.

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[1] Read before the Botanical Society of America, December 1906; abstract published in Science N. S. **25**: 282, 283. 1907.

[2] STRASBURGER, E., Die Coniferen und die Gnetaceen. 1872.

[3] STRASBURGER, E., Ueber Zellbildung und Zellteilung. 1876.

[4] STRASBURGER, E., Die Angiospermen und die Gymnospermen. 1879.

[5] JACCARD, P., Recherches embryologiques sur l'*Ephedra helvetica*. Inaugural Dissertation. Lausanne. 1894.

The present study of the fertilization and embryogeny of *E. trifurca* is the continuation of the paper[6] which dealt with spermatogenesis and oogenesis in the same species. Material for the study was collected at Mesilla, New Mexico, chiefly in April 1904. Much of the material collected in 1903 was unfit for a study of fertilization stages because of the ravages of a parasitic insect which attacked the ovules about the time of pollination. Embryos having been observed about April 20, 1903, it was hoped that by beginning to make collections as early as April 1 in the following season and continuing them at intervals of two days a fairly complete series could be obtained. Collecting was discontinued April 20, 1904, at which time the majority of embryos had attained their maximum size. The season of 1904 was unprecedentedly hot and dry and in consequence development was much accelerated, so much so in fact that embryos with large secondary suspensors were found in the material collected April 1. Not all of the material collected at the earliest date had been pollinated. In 1905 staminate strobili sent from the Carnegie Desert Laboratory, Tucson, Arizona, made possible the final study of the male gametophyte.

POLLEN TUBES AND FERTILIZATION

Pollen grains were placed in a ten per cent. solution of saccharose on a slide in a moist chamber. By evaporation the solution became considerably denser toward the close of the experiment. Shortly after being placed in the sugar solution, the fluted exine is ruptured by a longitudinal split extending along one side of the grain from end to end, and the intine with its contents is completely freed. The two prothallial cells soon disappear and the cytoplasm of the prothallial end becomes very vacuolate. The body cell next divides, the spindle being parallel with the long axis of the pollen grain (*fig. 1*). At the same time the tube nucleus and the stalk cell, which lie at opposite ends of the grain, each move through ninety degrees and lie side by side, or occasionally they may lie as shown in *fig. 2*. The tube nucleus comes to rest against the wall, assumes a lenticular shape, and soon afterward the pollen tube is put out from this point of contact. Appearances seem to indicate that the pollen tube is produced at the point of separation of the tetrads, but this could not be definitely determined because of the symmetry of the pollen grain and the possibility of a slight rotation of the extruded mass after escaping from the exine.

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[6] LAND, W. J. G., Spermatogenesis and oogenesis in *Ephedra trifurca*. BOT. GAZETTE **38**:1–18. *pls. 1–5.* 1904.

The male nuclei are of equal volume and are truly elliptical. One of them almost invariably passes in advance of the stalk cell, which takes a position in advance of the rearmost male nucleus (*fig. 3*). Measurements of male nuclei show them to be exactly of like dimensions; neither is there any optical difference. Their relative position in the pollen tube is the only evidence, if evidence it be, of any inequality. There is little doubt that the male nucleus nearest the end of the tube will succeed in fusing with the egg nucleus because of its favorable position. Within ten hours from the time the pollen grains were placed in the sugar solution the pollen tubes were sufficiently long to reach the egg. After twenty-four hours the tubes ceased to elongate, at which time they were three to four times longer than is necessary to penetrate to the egg. The stalk nucleus is usually about half the diameter of the male nucleus. The tube nucleus is variable in form, as is common among tube nuclei of gymnosperms.

As has been shown in the study of spermatogenesis and oogenesis, the pollen grains come to rest on the bottom of the pollen chamber in contact with the gametophyte, in the vicinity of or on the necks of the archegonia. Occasionally pollen grains rest on the sides of the pollen chamber as well as on the bottom, but by far the greater number rest on the bottom, and in consequence the pollen tubes are put out directly into the archegonia. Since all material studied was fixed at least four days after pollination, and fertilization is possible within ten hours after pollination, it has been very difficult to secure fertilization and early proembryonal stages. Only those ovules which have been incompletely pollinated by having the pollen lodged for a time in the long tubular micropyle, and later dislodged and reaching the pollen chamber, can by any possibility show fertilization. From the nature of things such a delay in pollination must be very rare, although the ovules are peculiarly fitted to have such delays occur. Among over 2800 ovules sectioned at the time when fertilization was expected, only two (*figs. 4* and *5*) showed early stages.

The pollen tube forces its way between the neck cells of the archegonium, rarely destroying them in its passage. Only in one or two instances were the lower neck cells destroyed. In *fig. 4* the lower and apparently double nucleus shows the all but complete fusion of the sperm and the egg nuclei. The small nucleus lying immediately above the fusing nuclei is the ventral nucleus; the one immediately above it is the second male nucleus, which in this instance has passed deeper into the egg cytoplasm than usual. *Fig. 5* shows the fusion nucleus with fragments of the ventral nucleus lying above it. The second male nucleus, with the stalk nucleus and tube nucleus lying immediately below it, is seen in the upper end of the egg. The stalk nucleus and the tube nucleus soon disappear. The second male nucleus does not ordinarily penetrate deeper into the egg than is shown in *fig. 5*, but undergoes its final changes here. The dense mass of cytoplasm surrounding the fusion nucleus and extending downward through the egg is well shown in *figs. 4* and *5*. This mass first appears as a densely staining spherical body in the upper third of the central cell, and disappears with the formation of proembryos.

EMBRYOGENY

The fusion nucleus gives rise to eight free nuclei, more or less unequal in size, and three to five of the largest ones surround themselves by a wall and produce embryos. The free nuclei are either arranged in a row down the middle of the egg, or more frequently are scattered through it. The lower ones in general successfully produce embryos, although a few instances were noted in which the lower ones did not function further than the one-celled stage, the micropylar ones alone being successful. Nearly all of the largest vacuoles in the egg disappear shortly after fertilization, and the cytoplasm becomes more and more homogeneous as free nuclear division progresses. The proembryonal nuclei usually become so dense that they can be seen with difficulty in the cytoplasm.

Delicate cytoplasmic radiations, similar to those figured in the unfertilized egg, stream out from each nucleus and end in a denser ring of cytoplasm. This delicately radiating cytoplasm becomes more and more vacuolate, finally taking on the appearance shown in *figs. 6* and *7*. In *fig. 6* the large cell is one of two proembryonal cells which later will produce suspensors. *Fig. 7* shows two or four functioning proembryos. The first suggestion of walls, or rather cytoplasmic thickenings, is shown in *figs. 6* and *7*. The functioning proembryos isolate themselves from the surrounding cytoplasm as follows. Cleavage cracks appear, starting presumably at the equatorial region of the last spindle, although all trace of a spindle has disappeared before cleavage is apparent. An early stage of incomplete cleavage between sister cells is shown in *fig. 8*. The cleavage cracks, following the feebly defined wall or cytoplasmic thickening, continue until they meet around the nucleus, carving out a more or less irregular mass of cytoplasm for each nucleus. Three of five completely isolated proembryos are shown in *fig. 9*, which also shows masses of egg cytoplasm that have not been appropriated by the proembryonal cells.

At the time the proembryonal cells have freed themselves completely from the egg cytoplasm they lie in a nutritive mass derived from various sources. Shortly after fertilization, the walls of the jacket cells, which always have been extremely tenuous, disappear and in most preparations the jacket-cell cytoplasm becomes mixed with that of the egg (*fig. 9*). Shortly before the walls disappear the jacket cells become binucleate, the nuclei dividing either mitotically or amitotically. Occasionally mitotic divisions occur simultaneously in every cell of both layers of the jacket, or every division may be amitotic, or both kinds of division may occur in the same jacket. When the latter occurs, the nuclei at the upper end of the archegonium divide amitotically, and these amitotic divisions can easily be mistaken for fusion. Occasionally the jacket nuclei enlarge, fragment, and their chromatin is scattered through the cytoplasm of the jacket cell and later passes out into the egg cytoplasm. Sometimes this fragmentation is accompanied by kinoplasmic fibers, as shown in *fig. 10*. *Fig. 9* also shows an intact jacket-cell nucleus which has passed into the egg cytoplasm. Occasionally, though rarely, instances were noted in which the jacket cells do not become binucleate and break down at the time of fertilization; some of them, especially those near the middle of the archegonium, have the nucleus surrounded by delicate cytoplasmic radiations similar to those noted in the unfertilized egg. These nuclei also very much resemble the egg except in size, being of course much smaller. Apogamy was at first suspected, but further study showed that these egglike jacket nuclei do not function, being finally broken down and absorbed by the embryos.

The second male nucleus is normally in the position shown in *fig. 5*. It enlarges and occupies the upper part of the egg and extends into the space recently filled by the adjacent jacket cells. The chromatin is arranged in strands, at the ends of some of which it may be aggregated in small groups (*figs. 6, 7*). The nuclear membrane breaks down on one side (*fig. 6*) and cleavage planes pass up into the nucleus. *Fig. 7* shows a male nucleus with an irregular mass of spindles with groups of chromatin granules at the poles. Later the region occupied by the male nucleus is filled with a number of small cells which may have come from further division of the second male nucleus, or some of them may be a joint product of chromatin from the male nucleus and from the jacket nuclei. Below this region are numerous small cells which possibly may have resulted either from further division of the functionless proembryos, or by division of the jacket nuclei which have wandered into the egg cytoplasm or from both sources, and still others from masses of cytoplasm which may have been separated into smaller masses of cytoplasm by cleavage planes, as shown in *fig. 9*. Numbers of the very small cells seem to have a single granule in the center; others appear to be only masses of cytoplasm. This nutritive mass, presumably derived from so many sources, is very ephemeral and is quickly absorbed by the functioning proembryos.

In the ephemeral nutritive mass in which the proembryos lie it seems that we have at least a suggestion of the origin of endosperm. The term endosperm is here used in the strict angiosperm sense and must not be confused with the female gametophyte of gymnosperms. Many things lead to the belief that the chromatin of the second male nucleus, together with that of the jacket nuclei, has something to do with the production of at least a part of the mass of small cells which appears in the egg and jacket region. It is at the edge of the disintegrating male nucleus that spindles first appear, with either a few granules or masses of chromatin at their poles. The absolute equality of the male nuclei, for they differ in no visible way except in position in the pollen tube, seems to suggest that the nucleus which does not fuse with the egg nucleus functions in some other way; for cells which cease to function are either eliminated or show signs which point to their future elimination. If it can be shown beyond doubt that the chromatin of the second male nucleus together with some of the jacket-cell nuclei or the chromatin from these nuclei are jointly responsible for some of the small cells in the egg and jacket region, it follows that we have the foreshadowing if not the real beginning of endosperm. At least it may for the present be designated as physiological endosperm. The apparently universal occurrence of triple fusion in angiosperms seems to preclude the possibility that they may furnish a solution for this problem. It is not impossible that the Gnetales, which in so many ways have reached the angiosperm level, may have some member which will give an answer to the problem of the origin of the angiospermic endosperm. The ephemeral mass of nutritive cells is certainly larger in *E. trifurca* than the endosperm mass of many angiosperms.

The functioning proembryonal cells round out as the adjacent nutritive mass is absorbed (*fig. 10*). The nucleus of a proembryonal cell divides, giving rise to two free nuclei, which at first are equal in size, but one soon gains an ascendancy over the other, becoming noticeably larger. A large vacuole develops in the upper part of the cell and the free nuclei pass down and to one side of the cell if it is one of the upper proembryos, but to the bottom if it is the lowest one in the archegonium. The larger nucleus is invariably placed lowest in the cell. Two papillae, seemingly initiated by the nuclei, are put out by the cell wall from the points nearest the nuclei (*fig. 11*). Soon the papilla nearest the larger nucleus rapidly elongates and the other papilla disappears (*fig. 13*). In one instance four free nuclei, one large, two smaller, and one very minute, were observed in a proembryonal cell. The suspensor tube is immediately directed downward toward the antipodal region if the cell is the lowest one in the archegonium, but outward and then downward if from one of the upper cells. *Fig. 13* shows the suspensor tube before either of the nuclei has entered it. The larger nucleus passes down nearly to the end of the suspensor tube, and immediately behind it a cleavage ring, beginning at the wall of the suspensor tube and gradually extending inward, appears in the cytoplasm and separates it into two masses, each containing a nucleus. *Fig. 14* shows the cleavage ring incomplete; and *fig. 15* is a much higher magnification of the same section. A wall separating the suspensor tube into two regions is then established at the cleavage plane.

The nucleus left behind (*fig. 14*) enlarges, enters the suspensor (*fig. 16*), becomes the suspensor nucleus, passes down, and remains in the lower end of the suspensor (*figs. 17, 18*), where it finally disintegrates (*fig. 19*). The suspensor quickly elongates, thrusts the embryo initial deeply downward into the gametophyte, and remains turgid until the secondary suspensor appears (*fig. 23*), when it collapses. The longest suspensor noted reached a length of 3.1^{mm}.

The nucleus of the embryo initial cell divides and a transverse wall is laid down in the usual way along the cell plate (*fig. 18*). *Fig. 19* shows a two-celled embryo with the wall fully established. An anticlinal division of the basal cell next occurs, the wall being either parallel with the suspensor (*fig. 21*) or slightly inclined (*fig. 20*). *Fig. 22* is immediately before the differentiation of dermatogen, which is cut off early, as shown by *fig. 23*. The latter figure also shows the first appearance of the secondary suspensor, a later stage of which is shown in *fig. 24*. The secondary suspensor is added to by successive elongations of basal cells of the embryo and finally merges insensibly into the root cap. There are three stages of suspensor formation: the suspensor tube, initiated by the activity of the nucleus which finally becomes the embryo-initial nucleus; the single suspensor, derived from the basal portion of the suspensor tube; and lastly the secondary suspensor ("le columelle" of JACCARD), derived from the basal cells of the embryo.

Coincident with fertilization and development of the proembryos, the gametophyte is stimulated to further activity. A single plate of the outermost layer of cells of the gametophyte, forming the bottom of the pollen chamber and extending outward a short distance under the tip of the nucellus, becomes meristematic (*fig. 25*), and by repeated periclinal and a few anticlinal divisions forms a plug which effectually closes the pollen chamber and receives the backward thrust of the elongating cells of the gametophyte and later of the embryo; this plug persists until absorbed by the maturing embryo. The antipodal region begins active division and the bulk of the gametophyte is materially increased. The cells near the archegonia first elongate, followed successively by groups of cells extending across the gametophyte. The elongated cells after having lost their contents are folded back and forth in the micropylar region (*fig. 25*), being prevented from escaping through the pollen chamber by the pollen-chamber plug. This elongation of groups of cells, proceeding successively from the micropylar to the antipodal region, serves admirably to keep an abundance of food constantly near the embryo.

As the seed matures the integuments and nucellus become gorged with food. The epidermal cells, especially those of the nucellus, are filled with starch and become so turgid that they are frequently torn loose from the layer beneath (*fig. 26*).

In the collection which reached Chicago on May 11, 1903, numbers of young plants were escaping from strobili still attached to the stem. This shows that under conditions favorable for growth the period of rest of the seed of *E. trifurca* is a brief one, if indeed it has a resting-period.

Staminate and ovulate strobili were first recognized in December, but they had probably been set the preceding month and perhaps earlier. The time from the setting of the strobili to the "germination" of the seed is therefore approximately six months. Compared with pines the time is short, for the latter require about thirty-six months.

DISCUSSION

The ovulate strobilus of Ephedra is compound, a character common to all Gnetales and shared by the Coniferales. The staminate strobilus, as in other Gnetales, is also compound, a character not found in other gymnosperms. Perhaps the nearest approach to a compound staminate strobilus outside the Gnetales is the short branch of *Torreya taxifolia*,[7] which bears a simple staminate strobilus in the axil of each leaf of the short branch. It is conceivable that by shortening the internodes in such a branch, combined with a further reduction of the sporophyll number, a compound strobilus will result; it is at least suggestive of the way in which staminate and ovulate compound strobili may have originated.

The two integuments of the ovule of Ephedra, a character shared with the Taxineae, may be regarded as a primitive condition, a condition even more primitive than in Taxineae, for the nucellus is free for a considerable part of its length. Also the inner integument first appears as two parts, and the outer as four, each distinct in origin. The tendency in both gymnosperms and angiosperms seems to be toward union of the two integuments into one.

The male gametophyte of *E. trifurca* shows a primitive condition in that it has retained two persistent prothallial cells. A comparison with the other groups of gymnosperms shows that in Cycadales the male gametophyte is less primitive in that it has retained only one prothallial cell, with perhaps occasionally another very evanescent one. Ginkgoales have one persistent and one evanescent prothallial cell. In Coniferales the Taxaceae and the Pinaceae show all grades in reduction of prothallial cells; *Podocarpus Hallii*, now being studied in this laboratory by Mr. L. L. BURLINGAME, frequently has as many as eight prothallial cells; Taxus and Torreya have none; Araucaria perhaps shows several prothallial cells; Pinus has two evanescent prothallial cells; and the Cupressineae none at all. According to PEARSON,[8] Tumboa has one prothallial cell. The testimony as to the Gnetums is doubtful; apparently some of them have one ephemeral prothallial cell and others none at all. *E. trifurca*, therefore, may be said to have retained a primitive character of its male gametophyte longer than Cycadales and Ginkgo, and longer than most Coniferales. It is possible that the number of prothallial cells will be found to vary in other species of Ephedra;

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[7] COULTER, JOHN M. and LAND, W. J. G., Gametophytes and embryo of *Torreya taxifolia*. BOT. GAZETTE **39**:161–178. *pls. A, 1–3.* 1905.

[8] PEARSON, H. H. W., Some observations on *Welwitschia mirabilis* Hooker *f.* Phil. Trans. Roy. Soc. London B **188**:265–304. *pls. 18–22.* 1906.

STRASBURGER found one prothallial cell in *E. campylopoda* and JACCARD none at all in *E. helvetica*. The technique is difficult and it is not safe to assume the absence of prothallial cells until a very large number of thin sections have been studied. The Gnetales as a group appear to have retained the primitive character of the male gametophyte along with a very high degree of specialization of the female gametophyte. In general a form showing a number of highly specialized characters may be expected to have primitive characters still lingering somewhere, perhaps because of the very high specialization of the majority of structures.

The usual number of sperms or male nuclei in gymnosperms is two. That this reduced number is derived from a gymnosperm condition in which more than two sperms or male nuclei were produced in a single pollen tube is very probable. The comparative study of antheridia and archegonia of bryophytes and pteridophytes shows that the antheridium is less conservative than the archegonium. Possibly the retention of the usual two sperms or male cells in gymnosperms is dependent upon the conditions under which they function. In gymnosperms the female gametophyte appears to have two tendencies; first to collect the archegonia into groups—archegonium complexes—in a common archegonial chamber; second, to reduce gradually the number of archegonia, maturing the few which are left earlier and earlier in the history of the female gametophyte, until they mature immediately after the free nuclear stage; finally, the free nuclei become eggs. The first-named situation, which perhaps after all may be only one of the stages in the last-named series, is best shown by the Cupressineae; the second tendency is illustrated by the taxad-Gnetales-angiosperm series. In Cycadales the sperms in each pollen tube, with one exception as yet, are two and equal, both being discharged into an archegonial chamber in which the archegonia are grouped; and each sperm has an equal chance to function. In Cycadales the archegonia are on the whole numerous, and that the archegonial group has resulted from the coming-together of scattered archegonia and that the tendency is further to eliminate archegonia is shown by the recent studies of *Dioon edule* by CHAMBERLAIN,[9] who finds from five to one archegonia in a chamber. An exceptional case was noted in which there were two archegonial chambers, each containing five archegonia; also instances were noted in which no archegonia were produced.

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[9] CHAMBERLAIN, C. J., The ovule and female gametophyte of Dioon. BOT. GAZETTE 42:321–358. 1906.

In Ginkgoales the two equal sperms are discharged into an archegonial chamber usually containing two archegonia, although occasionally three may be present; one functional and one abortive archegonium are not infrequent. Here, as in cycads, conditions are favorable for the retention of equality of sperms, at least for a very long time.

In Coniferales the situation is variable. In *Podocarpus coriacea*, COKER[10] found unequal male nuclei. The long-necked archegonia vary from six to ten and are separated from each other by one or more layers of cells; and the jacket cells do not go to pieces at the time of fertilization. Since a pollen tube discharges its contents into a single archegonium, only one male nucleus can possibly function. In Taxus[11] and in Torreya[12] the male nuclei are unequal, and the latter perhaps throws some light on the Ephedra situation. In Torreya the usually solitary archegonium appears as soon as walls are formed; even for a time after fertilization the walls are extremely tenuous, but show no tendency to break down. The gametophyte situation therefore closely resembles that in Ephedra.

In Pinus the numerous archegonia are scattered as in Podocarpus, but differ in that each archegonium has an individual archegonial chamber. The second male nucleus has no chance to function unless it may occasionally fuse with the ventral nucleus. The male nuclei are reported by COULTER[13] to be equal in *P. Banksiana;* CHAMBERLAIN[14] reports them equal in *P. Laricio;* while in *P. Strobus* Miss FERGUSON[15] reports them as unequal. An examination of Miss

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[10] COKER, W. C., Notes on the gametophytes and embryo of Podocarpus. BOT. GAZETTE 33:89–107. *pls. 5–7.* 1902.

[11] BELAJEFF, W., Zur Lehre von den Pollenschläuche der Gymnospermen. Ber. Deutsch. Bot. Gesells. 11:196–201. *pl. 12.* 1893.

[12] COULTER, JOHN M., and LAND, W. J. G., Gametophytes and embryo of *Torreya taxifolia.* BOT. GAZETTE 39:161–178. *pls. A, 1–3.* 1905.

[13] COULTER, JOHN M., Notes on fertilization and embryogeny of conifers. BOT. GAZETTE 23:40–43. *pl. 6.* 1897.

[14] CHAMBERLAIN, C. J., Oogenesis in *Pinus Laricio.* BOT. GAZETTE 27:268–280. *pls. 4–6.* 1898.

[15] FERGUSON, MARGARET C., Contribution to the knowledge of the life-history of Pinus. Proc. Wash. Acad. Sci. 6:1–202. *pls. 1–24.* 1903.

FERGUSON'S drawings, which show some of the male nuclei very irregular in outline, suggests the desirability that conclusions as to the equality of irregular nuclei should be based on volume rather than on optical sections. Perhaps the male nuclei of *P. Banksiana* and *P. Laricio* are more resistant to the conditions which cause elimination of supernumerary cells than is *P. Strobus*.

In Cupressineae the tendency to mass the archegonia in a common group finds its highest expression; in Thuja the further tendency to eliminate some of the archegonia is also apparent. In this group, with one notable exception, the male nuclei are two, and in all, so far as yet seen, are equal in volume and have equal chances to function. There are good reasons for believing that if few male nuclei were discharged into the complex the number of archegonia would be reduced gradually because of failure to function. In most of the Cupressineae the relatively high number of archegonia in a complex seems to be retained by having several pollen tubes reach the complex.

A member of the Cupressineae gave us the first proof of what seems to have been the primitive condition of the gymnosperm pollen tube. In 1904 JUEL,[16] studying *Cupressus Goveniana*, found sometimes four, more frequently eight to ten, and occasionally as many as twenty male cells in each pollen tube. JUEL considers the female gametophyte an abnormal one, for in one instance only did it get beyond the free nuclear stage and produce archegonia. The conditions which enable these numerous male nuclei to function are certainly ideal. In order to retain the large number of male cells which JUEL rightly considers a primitive gymnosperm condition, it seems that for some reason the female gametophyte of *Cupressus Goveniana* early lost its conservatism and went a step beyond the archegonium complex and formed free eggs. It certainly shows an interesting transition from archegonia to free eggs, and illustrates the tendency among gymnosperms to eliminate archegonia. The massing of archegonia and final elimination of walls must have taken place in *Cupressus Goveniana* while the male cells were still numerous, for in no other way does it seem possible to preserve the large number of male cells. That JUEL did not observe these free nuclei functioning in no way invalidates this conclusion.

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[16] JUEL, H. O., Ueber den Pollenschlauch von Cupressus. Flora 93:56–62. *pl. 3*. 1904.

In this connection it may be well to call attention to *Microcycas calocoma*, recently studied by CALDWELL,[17] which shares with *Cupressus Goveniana* the distinction of having retained a large number of sperms, sixteen being discharged from a single pollen tube. Large numbers of clustered archegonia are scattered all over the female gametophyte; also in numerous cases multinucleate archegonia were noted. This last condition seems to show that Microcycas while retaining archegonia has also only partially established septation among the free nuclei. The writer believes that the multinucleate archegonia of Microcycas are homologous with the "archegonial tubes" of Tumboa, and that the female gametophyte instead of being, as CALDWELL believes, the most primitive in cycads, has attained almost if not quite to the level of Tumboa. The same tendency to eliminate archegonia that is shown in all other groups of gymnosperms holds for cycads in a marked degree.

The Gnetales present practically an unbroken series illustrating the disappearance of archegonia and the coming-in of the embryo sac. In *E. trifurca* the long-necked, slightly scattered archegonia are very similar to those of Podocarpus. The antipodal end of the gametophyte is strikingly like the same region of Torreya, but the micropylar end shows an advance over Torreya in having the cells more loosely arranged and the jacket cells sometimes simulating eggs. The persistence of two equal male nuclei is perhaps due to the fact that the nuclei of the jacket cells in most cases become free. Another taxad character of Ephedra is the absence of resin ducts. It must not be assumed because of these resemblances to taxads that Ephedra, and of course the other Gnetales, are an offshoot from the Taxaceae.

A comparison of the female gametophyte of Tumboa shows a close resemblance to that of Ephedra in the antipodal region, but the micropylar end shows a very decided advance. PEARSON (*l.c.*) finds that the "corpuscula" described by STRASBURGER and by him considered as archegonium initials are in reality multinucleate. He calls them "prothallial tubes" and considers the micropylar region as even more highly specialized than in Gnetum. The evidence obtained from a study of the tendencies of the female gametophyte of all groups of gymnosperms leads the writer to conclude that the prothallial tubes of Tumboa are best regarded as partial septations among the free nuclei of the micropylar end, and that the condition shown by Tumboa is a necessary stage in the elimination of the archegonium and the evolution of the embryo sac. Such an explanation is in keeping with the tendencies of every gymnosperm group. Of the male nuclei of Tumboa we know nothing.

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[17] CALDWELL, O. W., *Microcycas calocoma*. BOT. GAZETTE 44:118–141. *pls. 10–13.* 1907.

In *Gnetum Gnemon*, according to LOTSY,[18] the female gametophyte has the antipodal region compact, with all traces of walls lost in the micropylar end, and the free nuclei all functional eggs. This is an advance over the partially septate condition of Tumboa. Two male nuclei are produced, but LOTSY is silent concerning their equality; from the condition under which they function there can be little doubt that they are equal. In the embryo sac of *G. Rumphianum* LOTSY found slight traces of septation. In the species of Gnetum investigated by KARSTEN[19] all trace of septation of the embryo sac is absent at the time of fertilization.

If we arrange a representative series of gymnosperms based on the female gametophyte alone, the series will be as follows: Podocarpus with its long-necked scattered archegonia; Torreya with usually a single archegonium appearing almost immediately after the free nuclear stage and having the antipodal and micropylar regions only slightly differentiated; *Ephedra trifurca* with from one to three long-necked archegonia with jacket cells sometimes simulating eggs, with antipodal and micropylar regions sharply differentiated, the former compact, the latter feebly walled; Microcycas with a loosely organized gametophyte at time of fertilization and having archegonia in clusters and also clusters of multinucleate archegonia which in the opinion of the writer, based on a comparative study of gymnosperms, are partial septations among free nuclei; Tumboa with free nuclei functioning as eggs in the partially septate micropylar end of the gametophyte; *Gnetum Gnemon* with the antipodal region compact and the micropylar region unseptate and containing free eggs; *G. Ula*, *G. ovalifolium*, and *G. verrucosum* with an embryo sac containing free eggs. *Cupressus Goveniana* is probably near the Tumboa level.

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[18] LOTSY, J. P., Contribution to the life-history of the genus Gnetum. Ann. Jard. Bot. Buitenzorg II. 1:46–114. *pls. 2–11.* 1899.

[19] KARSTEN, H., Beiträge zur Entwickelungsgeschichte einiger Gnetum-Arten. Bot. Zeit. 50:205–215, 221–231, 237–246. *pls. 5, 6.* 1892; also Zur Entwickelungsgeschichte der Gattung Gnetum. Cohn's Beitr. Biol. Pfl. 6:337–382. *pls. 8–11* 1893.

It seems that during the time the female gametophyte is passing from the scattered archegonium condition either to the archegonium complex or to the free-egg condition there will necessarily be a reduction in the number of male nuclei, because of the impossibility of more than one functioning as we now understand the meaning of the term function. When either the complex or the partially free-egg stage is reached, there can be no further reduction in the number of male cells remaining. From this it follows that the attainment of an advanced stage by one structure may result in the preservation of primitive conditions in another structure intimately connected with the highly specialized one. Research in forms showing some highly specialized structures is likely to uncover primitive conditions, which we are now too prone to dismiss lightly as "interesting abnormalities," but which are in reality stages marking progress.

The division of the fertilized egg to produce eight proembryonal nuclei is a common habit of gymnosperms. The failure of three to six of these free cells in *E. trifurca* is suggestive of the next stage, the direct production of a single embryo from the fertilized egg, which is characteristic of Tumboa, Gnetum, and angiosperms. That the old habit of producing several embryos is occasionally retained by Gnetum is shown by an observation by LOTSY, who says that occasionally, as the suspensor is pushing downward, branching of the embryo may occur.

The sporophyte characters of the Gnetales are so well known that it is needless to discuss them.

A comparison of all the characters of Gnetales seems to show that we have a fairly consistent group, the most primitive being Ephedra, the most advanced Gnetum, with Tumboa between, but perhaps nearer to Gnetum than to Ephedra. That the three are phylogenetically related seems certain.

There is no proof that the Gnetales have been derived from or are directly related to any living group. They have many characters of Coniferales, and if related to Coniferales at all it must be to the Taxaceae with which they have many things in common. Gnetales must be regarded as a modern group and the possibility of the derivation of angiosperms from them is of great theoretical interest.

SUMMARY

Ephedra trifurca is monosporangiate, but occasionally bisporangiate strobili occur.

The beginning of the staminate and ovulate strobili can be seen in December; the pollen is shed about April 1, and the ovulate strobili early in May.

The anthers, developing in acropetal succession on a compound strobilus, are surrounded by a perianth.

Two integuments, free from each other except at the base of the ovule, are present; the outer has four rudimentary bundles, the inner two.

The nucellus is free from the inner integument for more than half its length.

A conspicuous pollen chamber reaches down and lays bare the tip of the gametophyte, on which many of the pollen grains come to rest.

The pollen chamber is finally closed by a plug derived from the outermost layer of the gametophyte cells forming the bottom of the chamber; this plug prevents the escape of the embryo into the pollen chamber.

The pollen grain sheds its exine on contact with the mucilage in the pollen chamber or in culture media, and the body cell divides before the pollen tube appears.

Two male nuclei equal in volume and optical appearance are produced.

The female gametophyte is composed of two definite physiological regions, a loose micropylar and a compact antipodal one with haustorial cells at the base. A column of thin-walled cells containing much food extends from the base of the archegonia through the center of the gametophyte nearly to the haustorial region, marking out the line the embryo will follow.

Fertilization is possible within ten hours after pollination.

The walls of the jacket cells break down about the time of fertilization and their contents mingle with the cytoplasm of the egg; occasionally some of the jacket cells closely resemble the egg.

The second male nucleus disappears in the upper end of the egg and, as it disintegrates, minute cells appear, which are believed to be the joint product of the chromatin of the second male nucleus and the chromatin of some of the jacket cells; these minute cells at least foreshadow the endosperm of angiosperms, and may be called physiological endosperm.

The fusion nucleus gives rise to eight free nuclei, two to five of which produce suspensors.

Each functioning proembryo produces an embryo with a single suspensor.

Only one embryo reaches maturity.

If moisture is supplied the seed does not rest.

Six months elapse from the setting of the strobili to the "germination" of the seed.

Ephedra must be considered as the most primitive of the Gnetales.

NOTE.—Since this paper was in type, a paper by Miss BERRIDGE and Miss SANDY[20] on *E. distachya* has appeared.

They report the male nuclei as being inclosed in a common cytoplasmic sheath and markedly unequal. The functional nucleus slips from this sheath, but was not observed to function. Two kinds of embryos—normal and abnormal—are described; the former being essentially as described for *E. trifurca;* the latter, if the interpretation of the authors is accepted, is unique among gymnosperms. The nuclei of the jacket cells divide amitotically, escape from the cells, fuse in pairs, and produce proembryos. "In some cases the embryos are merely enlarged jacket cells which project into the archegonium." The writer has repeatedly observed in *E. trifurca* appearances which at the first glance might be interpreted as they are by these authors; but on careful examination and comparison in several thousand ovules they were found to be proembryos formed in the usual way. The ovule of Ephedra is so delicate that a slight pressure before fixation is almost certain to result disastrously to the structures.

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EXPLANATION OF PLATES XX-XXII

All figures were drawn with the aid of an Abbé camera lucida and reduced one-half in reproduction. Abbreviations are: m_1, male nucleus which fuses with the egg nucleus; m_2, male nucleus which does not fuse with the egg nucleus; s,

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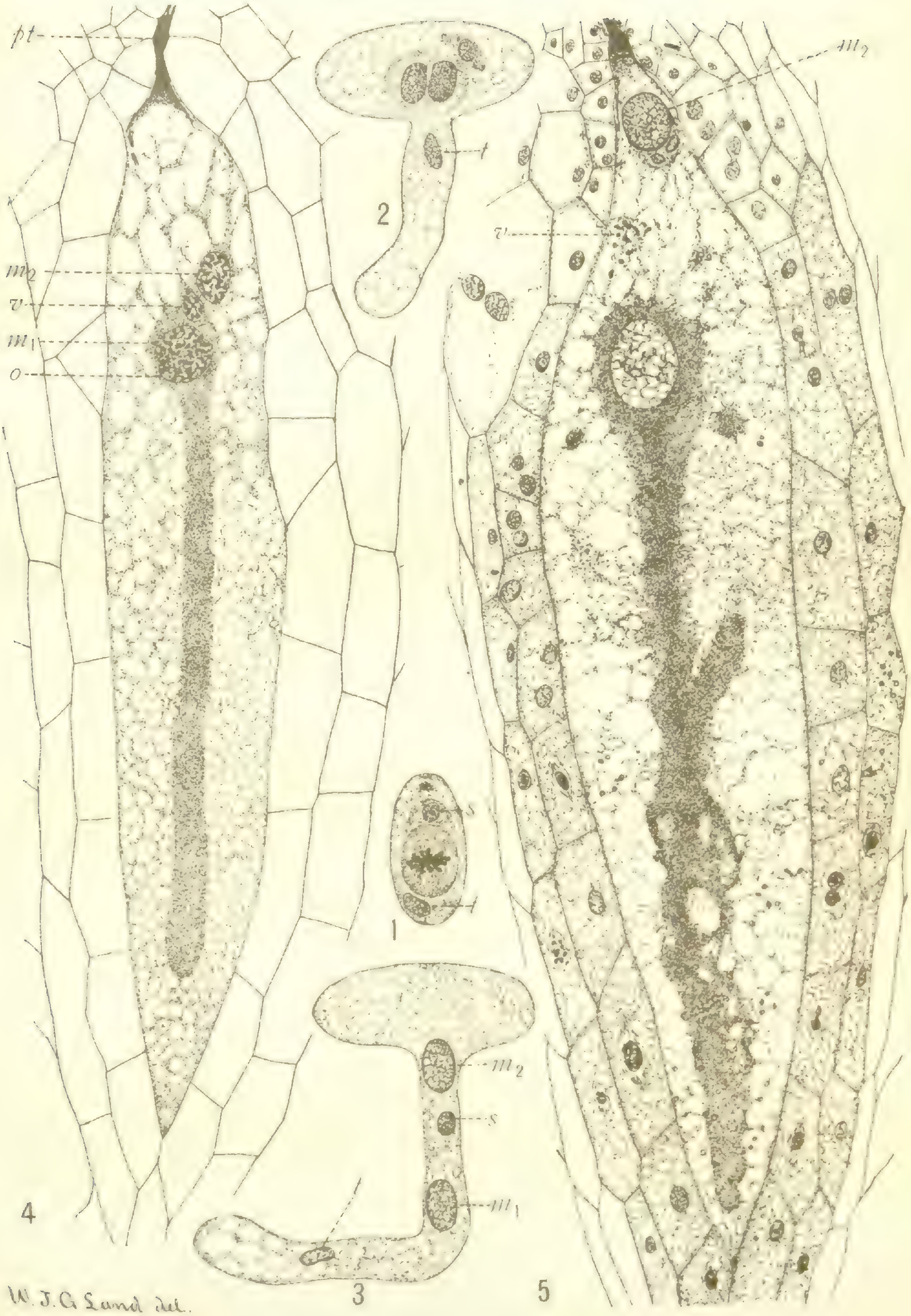
[20] BERRIDGE, ETHEL M., and SANDAY, ELIZABETH, Oogenesis and Embryogeny in *Ephedra distachya*. New Phytologist **6**: 128–134, 167–174. *pls. 2, 3.* 1907.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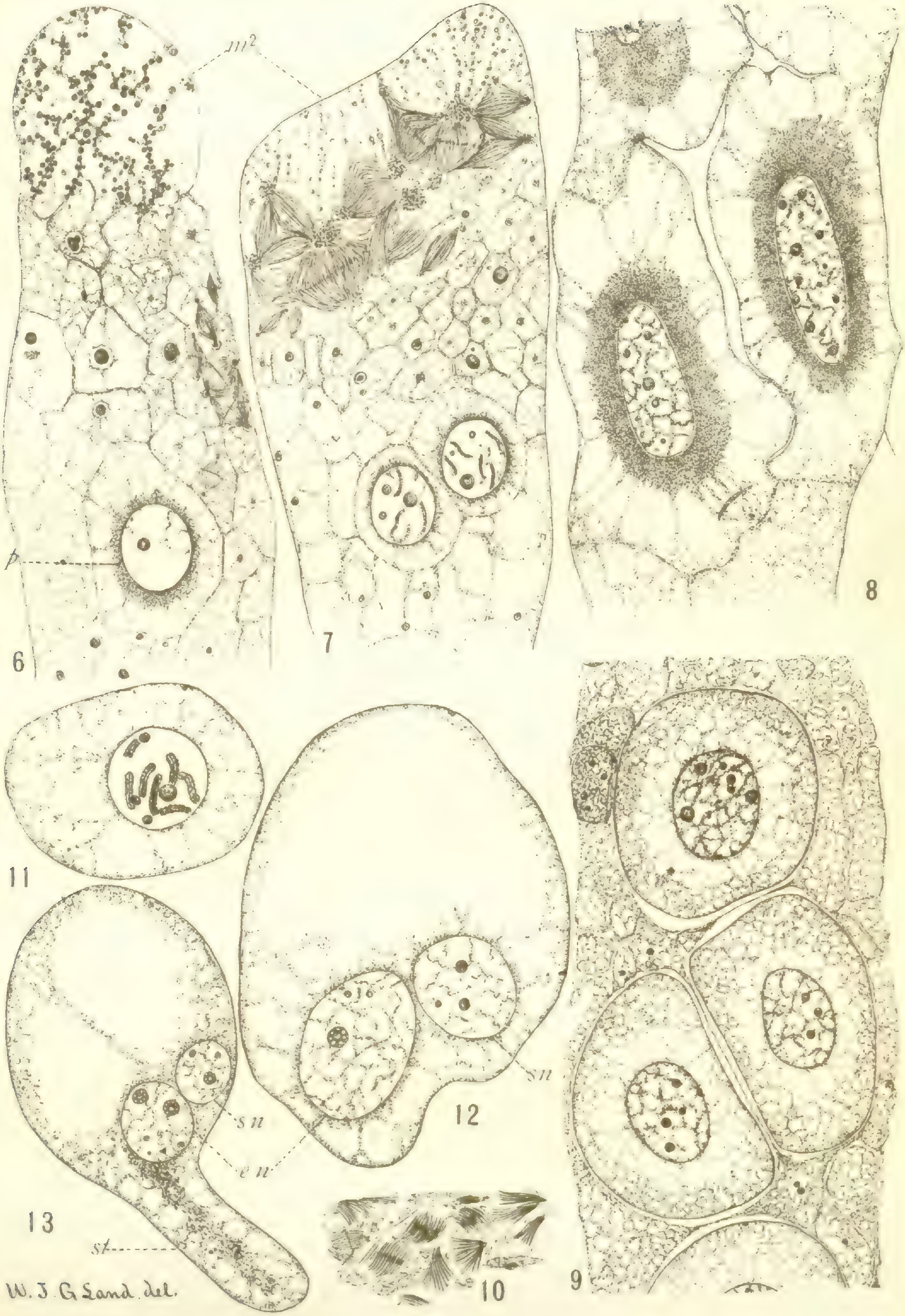
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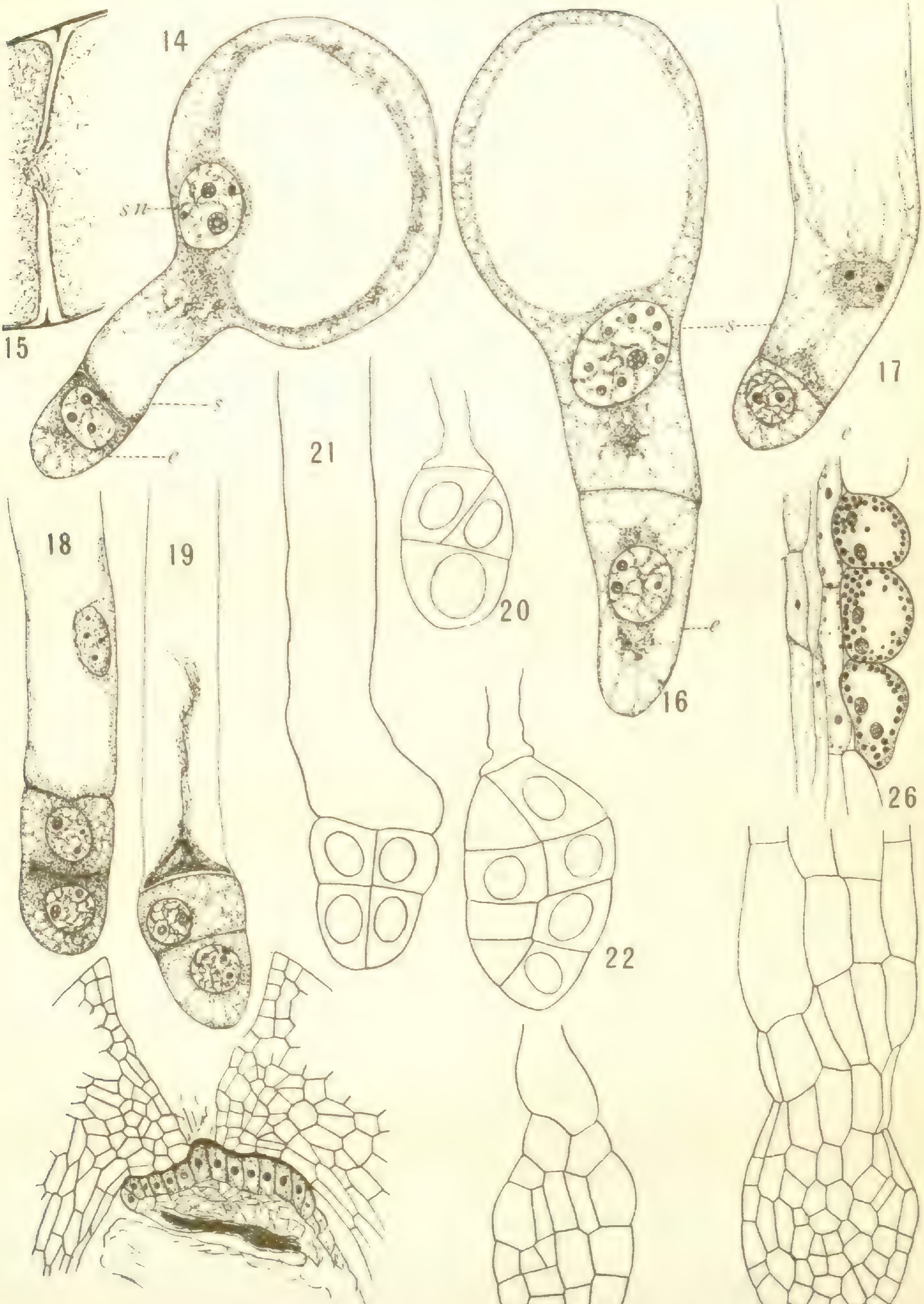
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stalk-cell nucleus; *t*, tube nucleus; *pt*, pollen tube; *o*, egg nucleus; *v*, ventral nucleus; *p*, proembryonal nucleus; *st*, suspensor tube; *sn*, suspensor nucleus; *en*, embryo-initial nucleus; *s*, suspensor; *e*, embryo-initial cell.

PLATE XX

FIG. 1. Division of the body cell. ×500.

FIG. 2. Pollen tube with tube nucleus entering the tube; in the pollen grain are the two male nuclei lying side by side, above and to the right is the stalk nucleus. ×500.

FIG. 3. Pollen tube which has attained the maximum length in saccharose solution. ×500.

FIG. 4. Median longitudinal section through an archegonium showing end of pollen tube, the fusion of a male nucleus with the egg nucleus, ventral nucleus, and the second male nucleus. ×250.

FIG. 5. Archegonium showing fusion nucleus, fragments of the ventral nucleus. the second male nucleus, and jacket cells, some of which are dividing amitotically. ×250.

PLATE XXI

FIG. 6. Upper end of egg, showing second male nucleus, small cells derived from various sources, and one of two functioning proembryos. ×500.

FIG. 7. Upper end of egg showing a stage of the second male nucleus slightly later than in *fig. 6*, the small ephemeral cells, and two of four functioning proembryos. ×500.

FIG. 8. Proembryos, showing incomplete cleavage of the cytoplasm. ×500.

FIG. 9. Three of five functioning proembryos; jacket nuclei in the egg cytoplasm; free masses of cytoplasm; also masses of cytoplasm remaining after the proembryonal cells have been carved out. ×500.

FIG. 10. Disintegration of jacket cells. ×500.

FIG. 11. One of the proembryos before formation of the suspensor tube; the nucleus will shortly divide. ×500.

FIG. 12. Proembryo with two free nuclei and two papillae, the larger of which is the beginning of the suspensor tube. ×500.

FIG. 13. Proembryo with suspensor tube; the larger nucleus is the embryo-initial nucleus; the smaller will be the suspensor nucleus. ×500.

PLATE XXII

FIG. 14. Cleavage plane cutting off the embryo-initial cell from the tip of the suspensor tube. ×500.

FIG. 15. Detail of the cleavage plane separating the embryo initial from the suspensor. ×1900.

FIG. 16. A stage slightly later than *fig. 14*. ×500.

FIG. 17. Elongated suspensor with embryo-initial cell shortly before dividing. ×500.

FIG. 18. Division of embryo initial cell. ×500.

FIG. 19. A stage slightly later than *fig. 18.* ×500.

FIG. 20. Division of basal cell of the embryo; length of suspensor 1.84^{mm}. ×500.

FIG. 21. Division of apical cell of embryo. ×500.

FIG. 22. An embyro slightly older than *fig. 21;* length of suspensor 2.8^{mm}. ×500.

FIG. 23. Organization of dermatogen and beginning of the secondary suspensor; length of suspensor 3.1^{mm}, the longest suspensor found in any preparation. ×250.

FIG. 24. Embryo and secondary suspensor. ×250.

FIG. 25. Early stage in formation of the pollen-chamber plug. ×250.

FIG. 26. Epidermal cells of nucellus containing starch. ×250.

THE DEVELOPMENT OF THE SEED IN THE PONTEDERIACEAE

W. C. COKER

(WITH PLATE XXIII)

A chance section of the young seed of Pontederia made several years ago presented a peculiar appearance in the antipodal end of the endosperm that led me to make an investigation of seed development in this family. I have been able to study *Pontederia cordata* and *Heteranthera limosum* in some detail, and *Eichhornia crassipes* to a less extent. Collections of Pontederia have been made in South Carolina and New York for several years. All my Heteranthera and Eichhornia material was collected in Jamaica during August 1900.

Examination of the literature of this family shows but one title dealing with its embryology. In 1898 SMITH (**14**) published a rather full account of seed development in Eichhornia and Pontederia, and gave one figure of the embryo sac of Heteranthera. Oddly enough, he completely overlooked the interesting peculiarity that appears in the endosperm of all three of the above genera, but otherwise, where parallel, my work, with a few exceptions, agrees with his. As SMITH did not attempt to give the development of Heteranthera, I have made a careful study of its ovular growth as a comparison with his work on Eichhornia and Pontederia. In the last two genera I have confined myself to the origin and development of the endosperm, which has the same peculiarity in all three types. HOFMEISTER (**9**) devotes a few lines to the development of Pontederia, but does not mention two sorts of endosperm.

HETERANTHERA

The megaspore mother cell of Heteranthera is separated from the epidermis by a single tapetal layer, as is commonly the case in monocotyledons (*fig. 1*), and it reaches a very conspicuous size before its first division (*fig. 2*). The spindle of this division lies near the distal end of the cell, and cuts off a small upper and a large lower cell (*fig. 3*). Each of these now divides (*fig. 4*), and the result is a large, lower, viable megaspore, with three small potential ones above. The two upper spores may either lie side by side (*fig. 5*), or one over the other (*fig. 5a*), agreeing in this respect with Eichhornia (SMITH). The division line between the upper two cells is very obscure, and as the cells soon show a sign of disorganization the cell wall separating them soon becomes invisible. In Eichhornia, SMITH describes two methods of megaspore formation from the mother cell; one as I have just described for Heteranthera, and another in which "the elongation of the ovule is accompanied by an elongation of the primary sporogenous cell without division of the latter. . . . The subsequent divisions in the elongated sporogenous cell take place in quick succession." He further says, "From a study of a large number of cases, similar to figs. 14 and 15, I have been led to believe that the four mother cells when formed in this way are seldom, if ever, separated by walls." I have noticed nothing in Heteranthera to indicate that there are two methods of megaspore formation. Walls are always formed in both first and second divisions, and the divisions occur in all cases as I have described.

Almost as soon as formed, the large lower megaspore commences to elongate and encroach on the ones above it, and after destroying them it pushes on through the tapetum and reaches the inner edge of the epidermis (*fig. 6*). Division of the nucleus now takes place and the embryo sac is soon organized (*figs. 6* and *7*). The structure of the sac is perfectly normal at this time; the synergids are rather sharply pointed and are decidedly denser than the egg; the antipodals are quite distinct, though small. SMITH states that in both Pontederia and Eichhornia the antipodals are ephemeral, disappearing early, but I have found this not to be the case in either Heteranthera or Pontederia. The lower end of the sac where the antipodals rest develops scarcely at all in the subsequent growth of the ovule, and remains as a little projecting pocket from an apparent basal invagination (*fig. 9*). In *fig. 8* is represented a sac at about the time of fertilization. The definitive endosperm nucleus is very large and conspicuous, being in fact as large as the egg or synergids.

At the stage represented in *fig. 9* a cell wall is present, cutting off the lower end of the sac into a separate chamber. In this chamber are a number of endosperm cells in addition to the three antipodals which still occupy their little pocket. The origin of this lower tissue has not been determined in all stages for Heteranthera, but from its development in Pontederia there is no doubt that it arises from the division of the lower of the two nuclei produced by the first division of the definitive endosperm nucleus. A later stage of this lower endosperm is shown in *fig. 10.* The section shows five cells below the diaphragm in addition to the antipodals. It will be seen that the cells below are larger than those above the partition. As this tissue has been studied most carefully in Pontederia, I will not go into detail here in regard to it, as it seems the same in both cases.

The structure of the nearly mature seed of Heteranthera is of sufficient interest to warrant some description. The axial embryo extends nearly the whole length of the seed, and is surrounded by a large-celled endosperm, which, except in its immediate neighborhood, is densely packed with starch. In *figs. 11* and *12* are shown longitudinal and cross-sections of the seed coats and superficial endosperm. The nucellus is entirely destroyed except for the scarcely recognizable micropylar cap, and the aleuron layer of the endosperm lies in immediate contact with a heavy cellulose membrane secreted by the inner integument. The inner integument (**11**) is considerably crushed and its cells are so densely filled with deeply staining material that their outlines are not recognizable except in unusually favorable conditions. Beyond the inner integument is a still heavier cellulose membrane, represented by a white line in the figures. This membrane seems to be secreted by the cells of the outer integument, which remains permanently two layers of cells in thickness. The outer layer changes very little in appearance during the development of the seed, remaining thin walled and boxlike, with the long axis running parallel to the longitudinal axis of the seed. The cells of the inner layer, on the contrary, undergo great changes. They become much elongated, perpendicular to the long axis of the seed, and flattened in the contrary direction. The partitions parallel to the long axis of the cells are much higher at their ends than in the center, and their outer edges dip inward in a regular curve (*fig. 12*). As the cells of the outer layer follow this curve, the result is that the surface of the seed becomes channelled and ridged in a longitudinal direction. A longitudinal section of the seed taken near the top of a ridge would appear as in *fig. 11*. Taken in a channel it would be the same except for the height of the inner layer of the outer integument. At the time represented in the figures, which is shortly before the full maturity of the seed, these large cells are found to be multinucleate, with nuclei and protoplasm in apparently normal activity. In *fig. 12* five nuclei are shown in a single section; they seem to have been formed by ordinary mitotic division. Note that, contrary to what might be expected, they are on the outer side, where the cell walls are thin.

PONTEDERIA

As SMITH has followed the early development of the embryo sac in Pontederia, I have taken up its history at a point just preceding the formation of the endosperm. In *fig. 13* is shown a sac just before the division of the definitive endosperm nucleus. This nucleus lies very low, just above the antipodal pocket, and in this position it remains until its division. As a result of the first division, a cross-wall appears, cutting the sac into a large upper chamber and small lower one (*fig. 14*). The endosperm nuclei in each chamber now divide repeatedly and the protoplasm increases rapidly in amount. As already mentioned, the lower tip of the sac does not increase in size, and as the part above grows outward, and develops downward at the edges, the antipodal pocket comes finally to hang from the center of a considerable depression (*fig. 17*). The antipodals never divide, but they are not ephemeral, as described by SMITH. They are easily visible after cell walls have appeared in the endosperm.

In the upper chamber of the sac the development of the endosperm presents no great peculiarities; cell formation begins only after the sac has increased in size many times and the embryo has become conspicuous. In the lower chamber the protoplasm increases rapidly in extent and density (*fig. 17*), and the nuclei multiply by mitotic division until their number becomes quite large, fifteen appearing in the single section shown in *fig. 17*. Soon after cell walls begin to appear in the upper chamber, they are also formed in the lower, but in a much more irregular way. From the first the cells cut out of the basal endosperm are often multinucleate, while those above are uninucleate, as usual, when first formed. Another point of difference is that the cell walls in the antipodal endosperm soon become much thicker than in the tissue above (*fig. 18*). As the growth proceeds their nuclei become very irregular, stain deeply, and show a tendency to fuse together. The protoplasm also becomes much denser than that of the upper endosperm (*fig. 18*). In *fig. 19* are represented several cells of the antipodal endosperm more highly magnified; they are from a stage slightly later than represented in *fig. 18*.

As the maturity of the seed approaches, and the upper endosperm begins to be filled with starch, the cell contents of the lower endosperm show signs of disintegration. The nuclei become deeply staining and irregular masses, and the protoplasm loses its distinctive structure and begins to disappear. No starch was found in these cells at any time, and at the maturity of the seed they appear, like the cells immediately above them, empty and somewhat crushed at the tip of the embryo.

The number of cells in the basal endosperm may become quite large. I have counted as many as forty-five in a single section, and there must have been in that case at least two hundred.

The seed coats of Pontederia are very much like those of Heteranthera, except that the outer integument is three cell-layers thick, with the cells of the two outer layers thin and boxlike, and those of the inner of the same height throughout, giving a smooth, instead of ridged, surface to the seed.

EICHHORNIA

My material of Eichhornia was not sufficient to follow the development of the basal endosperm, but its presence is shown in my sections at several stages. It seems to be similar in every way to that of Pontederia and Heteranthera. The structure of the seed coats is exactly as in Heteranthera. The same figures would do for both.

CONCLUSION

In looking over the literature of the subject I find but a single case where a tissue similar to this has been described, and there its origin has not been determined in detail. BILLINGS (1) has found that in *Tillandsia usneoides* there is formed in the lower part of the embryo sac, just above the antipodals, a tissue which in structure and position much resembles that of the Pontederiaceae. He does not give the exact origin of this tissue, but says: "the nuclei resulting from the first divisions of the endosperm nucleus take position at either end of the sac, leaving, however, a few to form a thin parietal layer between. At the antipodal end, cell formation with walls begins at once, and a number of large cells form a tissue which stands out conspicuously in the cavity of the sac, which otherwise contains only a few free endosperm nuclei." Tillandsia is considered a near relative of the Pontederiaceae, and it does not seem improbable that the origin of this tissue is the same in both cases. A difference to be noted is that in Tillandsia the basal endosperm tissue, according to BILLINGS, is cellular from the first.

The appearance of the cross-walls at the lower end of the sac at the first division of the endosperm nucleus will at once recall a similar condition in Sagittaria (SCHAFFNER **13**), *Potamogeton pauciflorus* (WIEGAND **16**), and Ruppia (MURBECK **12**). In these cases, however, the nucleus in the lower chamber does not divide to form a tissue, as in the Pontederiaceae.[1]

In *Potamogeton foliosus*, according to WIEGAND (**17**), the young embryo sac has almost the same appearance as in Pontederia; but this structure is supposed to have come about in a different way. The wall that cuts off the lower end of the sac is derived from the division of one of the first four nuclei of the sac, its sister nucleus forming the three antipodals which occupy the little pocket below. The author thus regards the large nucleus which occupies the lower end of the sac as an antipodal, as it is the sister nucleus of the lower polar. No upper polar nucleus is supposed to be formed and the endosperm develops from the lower polar. This whole procedure is so peculiar that it seems open to some doubt until confirmed.

In *Potamogeton natans*, HOLFERTY (**10**) finds the embryo sac in general quite normal, but in two or three cases a large nucleus was discovered in the lower end of the sac, cut off above by a wall. He thinks it may have originated in the same way as I have described for Pontederia.

In *Castalia odorata*, *C. ampla*, *C. pubescens*, *Nymphaea advena*, *Brasenia purpurea*, and *Cabomba piauhiensis*, COOK (**5, 6**) has found that an antipodal haustorium, cut off from the rest of the sac by a wall, contains a large nucleus which has the same origin as in Pontederia. This is also just what is found in the case of *Saururus cernuus* (JOHNSON **11**), but in none of these cases does the lower endosperm nucleus divide.[2]

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[1] In Sagittaria, according to SCHAFFNER, it may divide once or twice.

In Limnocharis, according to HALL (**8**), the lower of the two nuclei formed by the division of the megaspore nucleus passes to the lower end of the sac, but does not divide to form antipodals and a lower polar nucleus. The upper polar nucleus, formed in the usual way, sinks to the lower end of the sac, and there divides without fusion (there being no lower polar). A cell wall resulting from this division cuts the sac in two. The nucleus left in the upper cell divides to form the endosperm, but the lower does not divide.

In both Naias and Zannichellia, CAMPBELL (**3**) has described a large nucleus near the antipodal end of the sac, which increases greatly in size, but does not divide. He did not determine the origin of this nucleus, but offers two suggestions, either that the large lower nucleus is the lower polar, or that it is the product of the first division of the definitive endosperm nucleus. The latter explanation seems most probable.

In *Elodea canadensis*, WYLIE (**15**) finds that there is generally present a large extra nucleus in the antipodal end of the sac. He says: "The sudden appearance of the extra nucleus in the antipodal group, when one has in mind the behavior of the polars, might suggest that these nuclei do not always fuse, and that one of them passes down to the lower end of the embryo sac and joins those in the antipodal pouch. The general evidence, however, is against this view. The irregular number of nuclei displayed here and the general arrangement of the cytoplasm about them would indicate that any increase in number has come from division among the antipodals, an activity in this region that often results from fertilization. In all embryo sacs studied at earlier stages the lower polar had passed out of the tip, and its return to the antipodal group seems improbable." Is it not more probable that this nucleus is formed as in Pontederia?

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[2] COOK mentions a single division occurring once in *Nymphaea odorata*.

This discussion might be indefinitely extended by referring to the numerous cases of chambered sacs and other peculiarities of the endosperm of dicotyledons, but homologies are so improbable in such details that it is not necessary to cite them further. A good exposition of this subject may be found in COULTER and CHAMBERLAIN'S *Morphology of the angiosperms.*

An increase in the number of antipodals by division of the original three has been reported in a number of families, but, so far as I can discover, an endosperm tissue of the origin and character here described for the Pontederiaceae has not been before described. Its closest approach is probably to be found in Tillandsia.

CHAPEL HILL, N. C.

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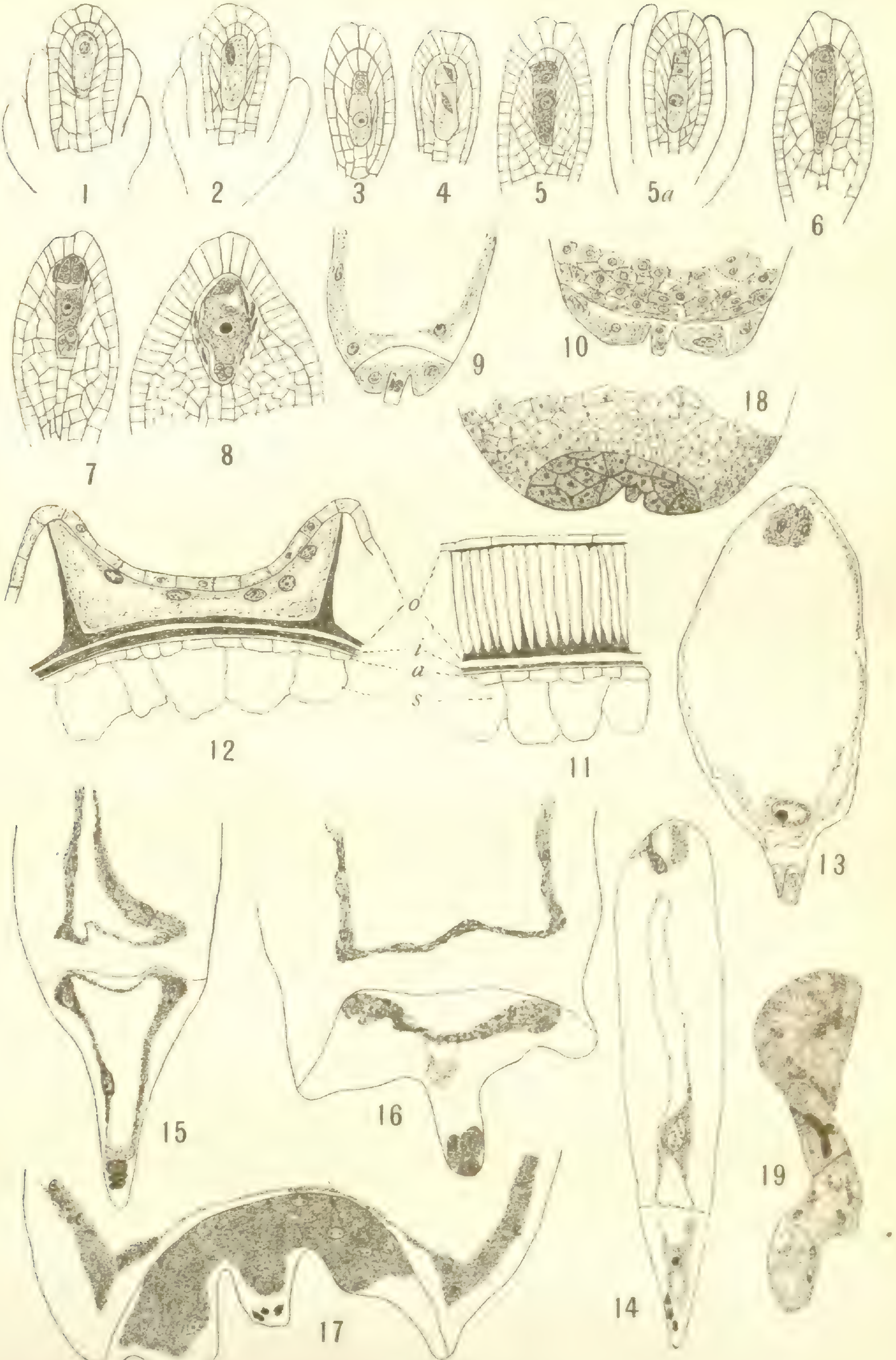
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COKER on PONTEDERIACEAE

EXPLANATION OF PLATE XXIII

The magnifications given are for original drawings, which have been reduced one-half in reproduction.

Figs. 1–12. Heteranthera limosum

FIG. 1. Young ovule, showing megaspore mother cell. ×675.

FIG. 2. Mother cell in division. ×675.

FIG. 3. Result of first division of mother cell. ×675.

FIG. 4. The two daughter cells dividing again. ×675.

FIG. 5. Shows four megaspores; the two upper side by side. ×675.

FIG. 5a. Four megaspores in a row. ×675.

FIG. 6. Four-celled embryo sac. ×675.

FIG. 7. Eight-celled embryo sac. ×660.

FIG. 8. Embryo sac ready for fertilization. ×675.

FIG. 9. Lower half of older embryo sac showing antipodals and basal endosperm. ×450.

FIG. 10. The same after formation of cell walls. ×450.

FIG. 11. Longitudinal section of seed coats and superficial endosperm. *a*, aleuron layer; *i*, inner integument; *o*, outer integument; *s*, starchy endosperm. ×780.

FIG. 12. Cross-section of same. Letters as in *fig. 11*.

Figs. 13–19. Pontederia cordata

FIG. 13. Embryo sac just before division of definitive endosperm nucleus. ×670.

FIG. 14. Embryo sac just after said division. ×670.

FIG. 15. Later stage showing antipodals, basal endosperm, and upper endosperm. ×670.

FIG. 16. Still later stage of same. ×670.

FIG. 17. Just before beginning of cell-wall formation in endosperm. ×670.

FIG. 18. Showing both kinds of endosperm after formation of cell walls. ×150.

FIG. 19. Several cells of basal endosperm at about the same stage as *fig. 18*. ×670.

BRIEFER ARTICLES

SOME NEW WASHINGTON PLANTS

In his *Species and varieties*, De Vries makes the following statement: "[The subgenus Onagra] seems to be rich in elementary species, but an adequate study of them has as yet not been made. Unfortunately many of the better systematists are in the habit of throwing all these interesting forms together, and of omitting their descriptive study." A small collection of Oenotherae recently determined at the Gray Herbarium for W. N. Suksdorf well exemplified the justice of this criticism, for although it lacked one of the two species of Onagra attributed to Washington in Piper's recent flora, it contained no less than three undoubtedly distinct species of this subgenus; one a very large-flowered plant of obvious relationship to *Oenothera Hookeri* T. & G., the second probably referable to *O. strigosa* (Rydb.) Mack. & Bush, the third a new species.

Oenothera (Onagra) **cheradophila** Bartlett, sp. nov.—Herba erecta ca. 1^{m} alta simplex vel in parte inferiore ramosa. Caulis vinaceo-purpureus deorsum albo-pilosus sursum subappresse strigosus. Folia caulina pallido-viridia lanceolata utrinque albo-strigosa; inferiora usque ad 3^{cm} lata 16^{cm} longa, apice acuta, basi in petiolum alatum brevem decurrentia, leviter remoteque denticulata, denticulis apice albis induratis; superiora parviora integerrima sessilia apice basique acuta. Bracteae foliis supremis similes sed eis parviores, maximae a capsulis maturis plerumque superatae infra mediam 6^{mm} latae 2.5^{cm} longae. Hypanthium 2.5^{cm} longum inferne ca. 2^{mm} crassum superne aliquanto crassius, extus patenter albo-pilosum. Calycis segmenta pallido-viridia densius subappresse albo-strigosa deltoidea 11–13^{mm} longa ad basin 4^{mm} lata, apicibus liberis, calyce nondum expanso, vix 1^{mm} longis acutiusculis. Petala flava saepe rosaceo-tincta 8^{mm} longa infra apicem 7.5^{mm} lata basi cuneata apice altiuscule retusa. Stamina corollam paulo superanta, filamentis planis ca. 6.5^{mm} longis sursum gradatim angustatis, antheris ca. 6.3^{mm} longis brevissime infra mediam affixis. Styli pars hypanthio exserta 2.5^{mm} longa. Stigma 4-partitum viride, ramis subteretibus carnosis ascendentibus 4^{mm} longis plerumque apices filamentorum vix attingentibus, raro paululo longioribus sed nunquam apices antherarum superantibus. Capsula matura prope basin 5–6^{mm} crassa 3^{cm} longa subquadrangula pallido- vel subolivaceo-viridis appresse albo-strigosa, ad apicem versus gradatim angustata et in rostrum 3^{mm} longum desinens; rostri segmenta, capsula dehisceta, recte divergentia. Semina brunneola prismatica 1.5–2^{mm} longa.

Type, *Suksdorf 5860* in Herb. Gray, low sandy river bank, Bingen, W. Klickitat County, Washington, 20 Aug. 1906. Other specimens which may be placed here are *J. S. Cotton 620*, sandy banks of river, Prosser, Yakima County, Washington, and (?) *L. N. Gooding 271*, river sand-bar, Middle Fork of Powder River, Johnson County, Wyoming. These were both distributed as *Onagra strigosa* Rydb., a clearly distinct species of which there is a cotype in the Gray Herbarium.

The strongest diagnostic features of the two plants are as follows:

OENOTHERA STRIGOSA	OENOTHERA CHERADOPHILA
Bracts twice or thrice as long as the mature capsule, obtuse at base.	Bracts almost always considerably shorter than the mature capsule, acute at base.
Flower bud and hypanthium ochraceo-vinaceous, with sparse spreading pubescence.	Flower bud and hypanthium greenish yellow, pubescence more dense.
Free tips of calyx segments (in bud) 3^{mm} long. Petals $1.5–2^{\mathrm{cm}}$ long. Color light yellow, fugaceous in wilting.	Free tips of calyx segments (in bud) less than 1^{mm} long. Petals 8^{mm} long or less. Color greenish yellow, intense, persistent after wilting.
Stamens shorter than the corolla.	Stamens usually slightly longer than the corolla.
Stigma a little exceeding the stamens, lobes flattish, spreading.	Stigma usually reaching only to end of filaments, teretish, ascending.

In the case of both species the measurements were made from typical flowers of type material. At the end of the inflorescence, or on weak lateral branches, both *O. strigosa* and *O. cheradophila* often bear flowers which are greatly reduced in size and in which the petals are disproportionately small. In such flowers of the former species, the stamens are likely to be longer than the petals.

It is worthy of note that very little of the material which western collectors have distributed as *Onagra strigosa* Rydb. matches the plant from Pony, Montana, which Rydberg designated as the type of his species.

LEWISIA PYGMAEA (Gray) Rob., var. **aridorum** Bartlett, var. nov., caudice foliisque radicalibus eis formae typicae similibus; scapis brevioribus robustioribus a foliis longe superatis. Bracteae lanceolatae margine glandulis subatris longistipitatis praeditae. Pedicelli 1–3 quam bracteae paulo, nunquam duplo, longiores. Sepala usque ad 5^{mm} longa late ovata vel orbicularia margine denticulata, denticulis in glandulas longistipitatas atras desinentibus. Petala (ut in forma typica ex loco eodem) alba, anguste oblonga quam sepala dimidio longiora apice etiam glandulas stipitatas 3–4 gerenta. Capsula turbinata atro-brunnea 4.5^{mm} longa.

Type, *Suksdorf 5725* in Herb. Gray, dry, bare places in meadows, Mt. Paddo (Adams), Yakima County, Washington.

Unusually well marked as a variety by the extreme development of stipitate glands on the bracts, sepals, and petals. The variation is perhaps induced by habitat, for the typical form of the species (except for the fact that it has white petals) occurs at the same altitude on the mountain, growing intermingled with the variety to some extent, but more abundantly "in damp or wet sandy places." It may be that all of the Mt. Paddo material constitutes a species, of which the plant above described is a variety, differing from *Lewisia nevadensis* in its denticulate calyx segments and from *L. pygmaea* in its white corolla. Until a more significant difference from *L. pygmaea* comes to light, such a treatment is hardly to be justified, for in at least one species of the genus, *L. rediviva*, the color of the corolla is known to vary from deep rose to pure white.—H. H. Bartlett, *Gray Herbarium.*

SOME PERPLEXITIES OF THE INDEXER

During the last few years the work on the *Card index of new species, varieties, and forms of American plants* has necessitated the examination of a large number of taxonomic papers of both American and foreign authorship. Some of the perplexing questions which have arisen I wish to bring before the botanical systematist. It may be urged, as one correspondent has already suggested, that "the scientist writes for the student and not for the indexer." This is true, but is it the whole truth? In these days of multiplicity of publications it is well-nigh impossible for each student of systematic botany to review carefully all the literature which may possibly bear upon his subject or contain a new name in the group upon which he is working. Not long ago a publication relating to a state flora and containing more than 600 pages was carefully examined, with the result that six new combinations were found; but there was no indication whatever that these were new. Can each student spare time for this? With the aid of such works as the *Index Kewensis*, the *Index to North American fungi*, the *Card index*, etc., the student readily turns to the original descriptions of the plants in the group which interests him, and from articles containing these descriptions he finds references to the important works relating to his specialty. He is also able to ascertain whether a name or combination which he proposes to launch as new has been used previously. The relation of the index to the systematist is that of a catalogue to the worker in a library. Now the scientist is not the person who will take his time for index work, and even if he did he would be limited to the few groups with which he is familiar, or should he undertake a larger field he would become, outside his specialty, only an indexer.

Indefiniteness and inaccuracy in publishing new names are the cause of much trouble to the indexer as well as the student, and result in many errors. One instance of this occurs where there is no indication to show that certain names in a given paper are new and many others cited in the same way have been published earlier. Even the student, in such cases, would be unable to discern the new from the old without the aid of indexes. Another perhaps just as misleading method of citation is to leave the "n. sp.," "in litt.," "in herb." or "MSS" attached to a name which has been already published. If the name appeared in the first edition of a work it is not a "n. sp." in the second edition; hence the inaccuracy. In 1894 Caloneis, a new genus of diatoms, was made. Under this new genus are 74 species, many of which are transferred from Navicula. Now, how are these species under a new genus given? One example, perhaps, will be sufficient: "*C. obtusa* W. Sm. (1853)." By reading the synonymy we learn that in 1853 W. Smith (who died in 1857) made the species *Navicula obtusa*, but he never heard of *Caloneis obtusa*, for the genus was not named until 1894, 37 years after his death. Is not then the citation "*C. obtusa* W. Sm. (1853)" misleading and therefore unscientific? Another form which gives rise to ambiguity is the unsupplemented use of the parenthetical authority. In many instances the author will cite the parenthetical author alone, leaving the author of the combination an unknown quantity. It may be a new combination, and if so the question arises whether a name can be considered published which is connected with no description and no synonym, but merely an authority given in parenthesis indicating that somewhere and some time during the last 150 years the author cited in parenthesis has used the specific name for this plant under another genus either for a species or variety. Too many examples might be given for this. In omitting the authorship of a combination some writers claim that the only one who should have the credit is the one who originally described the plant. The truly scientific worker does not think of credit, but he may well consider that the author of a correct combination is as important for reference to the future student as the author of the original name. Can it be that some authors omit their own names from new combinations because of modesty? In such a case why should the name be signed to the article in which they are published? When the authority of a combination is omitted there is no clue given to the place of the transfer, and one may search in vain without the aid of an index to find the date of the transfer or notes made in connection with it. Not infrequently the indexer must spend hours searching, at best with doubtful result, for an earlier reference to, or a correct synonym for, a combination used with parenthetical authority only. If it is so important to give the authority for the original description of a plant, is it not just as important to give the name under which it was described, and the name of the one who has placed it in the correct genus?

In 1753 Linnaeus established the binomial system of nomenclature and this was followed until very recently. Now, however, a few of our botanists have reverted to the use of the trinomial, and not only for their own new names, but in citing authors of the past. Thus Dr. Torrey, Dr. Gray, and many others who never used this form are credited with it. Recently one of our younger botanists published the name *Spilanthes americana*, var. *parvula*, forma *parviflora*. Would it be a correct citation of this name to make it *Spilanthes americana parvula parviflora*, or fair to the author to attach his name to a combination so pre-Linnaean? One great objection to the trinomial is the indefiniteness of the third part; some use it as a subspecies, some as a variety, some as a form, some as a mutation, etc., and the reader or student is often left without any clue to what category it belongs. In a paper recently issued the preface states that the rank next below the species is a subspecies, thus making the third name of the trinomials used in this paper rank as subspecies. The author proceeds to make the third name of all his new trinomials subspecies and then cites all varietal names made by earlier writers as the third name of a trinomial. Does he thereby transfer varieties to subspecies and make new combinations which the student of the future and the indexer must consider? Certainly the names were not used in this form originally.

Just the opposite of the last point is the use of the binomial in the index to a periodical when the name on the page to which it is referred is not in accord: for example, *Prunella vulgaris scaberrima* occurring in an article is cited in the index to the volume as *Prunella scaberrima*. Is the latter, then, a new combination? If so, who is authority for it, for the name of the one who indexed the volume is never given?

The errors and inaccuracies of the past must remain. But the present and future systematic botanists can easily avoid them in their forthcoming works by (1) indicating clearly each new species, combination, or name, (2) not allowing a name to appear as new when it has been published previously; (3) always giving the correct authority, or, where the parenthesis is used, the correct double authority; (4) stating clearly the category to which each name, below the specific, belongs; and (5) in no way distorting or altering the rank of names attributed to other authors.—MARY A. DAY, *Gray Herbarium.*

CURRENT LITERATURE

BOOK REVIEWS

Physiology and ecology

We take up Dr. CLEMENTS' new book[1] with favorable anticipations, ready to welcome a text of moderate size with the broad scope indicated by the title *Plant physiology and ecology.* The author tells us that the book is based upon his earlier *Research methods in ecology*, the manner of treatment being the same; i. e., first to consider the plant as an individual, establishing certain relations between the physical factors and its functions and form (physiology), and then to consider it as a member of a larger or smaller group of plants (ecology). "The proper task of physiology," says the author, "is the study of the external factors of the environment or habitat in which the plant lives, and of the activities and structures which these factors call forth. . . . . The sequence of study is consequently factor, function, form." So after selecting and describing some prominent factor—water, light, temperature, etc.—he proceeds to discuss its influence upon the various functions and organs.

Undoubtedly that method of treatment possesses marked advantages; but it may be seriously questioned whether our present knowledge is broad enough and exact enough to permit its successful use. And if it were, to write physiology in such a manner is peculiarly difficult. It requires thorough familiarity with the literature, especially that dealing with experimental morphology and irritability, clear conceptions of physical chemistry, and above all an instinctive avoidance of vague and inexact physiological cant. Certainly Dr. CLEMENTS' adoption of this method makes the physiological part of the book strikingly unconventional; the ecological part is less abnormal because ecology has proceeded from the first largely along such lines. And of the ecological part we have little to say, since it is essentially like that of the earlier book (reviewed in this journal, **40**:381. 1905).

Pedagogically the book leaves much to be desired. In the earlier sections the author wavers between textbook and manual; for beside the "experiments" in distinctive type (some of which are not experiments at all), the body of the text is partly subject-matter and partly directions to the instructor as to the management of his class, or to the student as to the materials and methods of his work.

In the very first chapter, on stimulus and response, the student is plunged into abstractions of which he can have no previous conception and regarding which he receives no adequate explanation. Thus, the tonic and stimulating action of external factors is discussed in a dozen lines on page 2 and nowhere else referred to. Distinctions the finest are drawn between normal and abnormal adjustment, adjustment and adaptation, growth and modification, that puzzle the reviewer; and it is hardly probable they would be more intelligible to the sophomore, for whom the book is intended.

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[1] CLEMENTS, F. E., Plant physiology and ecology. 8vo. pp. xv+315. *figs. 125.* New York: Henry Holt & Co. 1907.

Logically the arrangement of topics is sometimes peculiar. How is the student to comprehend the treatment of translocation and storage of food as an adjustment to light; and particularly in what sense can digestion, respiration, fermentation, the nutrition of non-green plants, growth, reproduction, pollen and pollination (treated at length), flowering, and fructification be looked upon as adjustments to temperature?

Dr. CLEMENTS is known as the proposer of many technical terms, of which few, fortunately, reappear in this book. But, what is even more confusing, he makes free to change the meaning of long-used terms. We had a pretty definite idea of what stimulus and response mean, but it does not fit when absorption, diffusion, transport, and transpiration are called responses to water stimuli. Imbibition is defined so as to include the entry of water into porous bodies. Cutinization is said not to coexist with epidermal hairs and is practically limited to xerophytes. The well-known actinometer masquerades as a photometer; heliotropic is distinguished from phototropic; chemosynthesis would never be recognized by the man who introduced the term; rootstalk, a word unknown to dictionaries, replaces the Anglo-Saxon rootstock. Aphototropic must surely be a typographic error, but nyct*o*tropic is doubtless an emendation. Reaction time and perception time have new and confusing definitions; but presentation time does not appear at all.

One serious danger inheres in Dr. CLEMENTS' method; there is a tendency to ascribe changes of function and form which have a very complex causation to a particular factor. One has only to examine the table of contents to find illustrations of this and the pages abound in examples. The offhand way in which some of the most elusive problems are settled by referring them to simple causes is appalling. The cause of cell division, the nature of polarity, the relation of turgor to growth, the mechanics of stomata are a few cases which the judge as it were dismisses with costs!

Many a pitfall, too, awaits the thoughtless in "explanations" which are merely a form of words that only cloak our ignorance. Absorption is "an inherent property of protoplasm;" "the need for the water of absorption increases toward the fibrovascular bundles," and "in similar fashion the demand for food materials increases toward the outer layers," so that "the general direction [of movement] is determined by these two *facts*" (sic?); the "stability of a species" prevents its modification in a new habitat—these are a few examples of meaningless phrases.

For the adopted mode of presentation an acquaintance with recent work is a *sine qua non*. Yet some statements have a curiously antique flavor. PRINGSHEIM's old screen theory of chlorophyll appears on one page and on the opposite one the modern theory is stated, but no decision as to their merits is reported. The amount of CO_2 in the air still appears as .04 per cent, and the starch formula as $C_6H_{10}O_5$. The work of two decades on solutions and osmosis is overlooked, for its bearing on the entrance of water, salts, and gases and on the movement of water and foods scarcely appears. The great advances in the last five years in the knowledge of perception, perceptive regions, and the interrelations of reactions find no reflection in this book, though they belong to its very essence.

Dr. CLEMENTS set himself a very difficult task; perhaps an impossible one, if we do not mistake the trend of recent study. That must be allowed for. Our main criticism, however, is not upon the choice of material for a brief treatise; it is against the attitude of mind that can tolerate vague explanations and invalid reasoning, and against a treatment of fundamental topics which is ineffective and not in accord with present knowledge.—C. R. B.

Jost's Plant physiology

When we reviewed this book in its original German,[2] we expressed the opinion that it was "easily the best work on plant physiology in any language, for the general student." Further use of it has confirmed this opinion, though it has at the same time uncovered some weaknesses that did not appear on the surface. It still remains as adequate a presentation of the fundamental features of plant activity as is likely to be made by any one author. Though it lacks the suggestiveness and comprehensiveness of PFEFFER, and can by no means replace that indispensable work, its clear and picturesque style adapts it better to the advanced student and teacher. Our hope that it would be translated into English has just been fulfilled. The Clarendon Press secured the right of translation and Professor HARVEY GIBSON, of the University of Liverpool, is responsible for the work.[3]

There has been no editing of the author by the translator. Even the index is a translation. Dr. JOST himself has added some notes and embodied some corrections; but these are relatively few and brief, and might well have been a more marked feature of the English edition.

A literal translation was the aim, says the preface, but that certainly has not been attained. It is not difficult to find passages where wholly gratuitous changes have been made, qualifiers added or omitted, or variant expressions used, that leave the phrase far from a literal translation. For example: "hochstens ganz gelegentlich musste erwähnt werden . . . ." is rendered "we drew special attention to the fact . . . ." when the fact *was* only incidentally mentioned; and "wachstumsfördernde Wirkung" appears as "stimulating effects," with growth not alluded to in the context. "Quite, or almost quite, impermeable" for "sehr schwer oder gar nicht permeabel" surely must be a typographic slip for "almost or quite impermeable." When JOST wrote "der im Wasser gelösten Moleküle und Ionen," why should it be translated, "of the molecules dissolved in water and of the ions," as though the ions were not dissolved in water? There are other slips of more serious nature. Thus, in describing the cohesion movements of the annulus of ferns and the anthers of seed-plants, to render "Füllwasser" by "imbibition water" makes the description inconsistent and unintelligible, for it is the water contained in the cell cavity, not the imbibed water of the walls, whose tension comes into play.

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[2] BOT. GAZETTE 37:390. 1904.

[3] JOST, LUDWIG, Lectures on plant physiology. Authorized English translation by R. J. HARVEY GIBSON. Imp. 8vo. pp. xiv+564. *figs. 172*. Oxford: Clarendon Press. 1907. Cloth 21 *sh.*, morocco 24 *sh.*

If these defects appear in a cursory examination one may suspect that a thorough comparison would reveal many others. Yet the total impression, without such a search, is quite the reverse, and it may be fairly said that on the whole the translation, though rather wordy, is good. The English may not be irreproachable, but it happily does not fall into the German idiom.

We note JOST'S lame excuse for retaining assimilation instead of adopting photosynthesis, pleading bad examples and the lack of a correlative term to apply to "nitrogen assimilation." A little boldness, pardonable in a leader, would have set aside the examples of PFEFFER and WIESNER, and a little ingenuity would have devised a new term, if amide synthesis and proteid synthesis were not acceptable. A bit more boldness in the translator would have at least harmonized the typography of citations with the better style of the original, and not overmuch would have modernized it completely. Now it halts between the traditional and the modern, losing much of the modest advance the author had made.

In makeup the book follows the general style of the Clarendon Press classics. The thicker but lighter paper, the solid type and slightly larger page, make a bulkier book, actually larger by some 60,000 words, fall within the compass of 554 pages of text as against 682 in the original. The rough-surfaced paper makes impossible the proper printing of the delicate cuts of the German edition, the halftones especially being mere smudges. The figures should have been remade for such paper. Yet we can almost forgive the blotchy cuts for the sake of the dull surface and the agreeable lightness of the book. But the price, as usual, goes away up—21 to 24 shillings as against about 15 marks—and imported copies at $7.75 will be almost too dear for general students. Yet it is well to have it available in English even at the exorbitant price.—C. R. B.

The morphology of plants

DR. JOS. VELENOVSKÝ[4] has added to the lengthening list of general textbooks on plant morphology. Every such work represents some characteristic point of view, and that of VELENOVSKÝ seems to be that of the older morphology tinctured by a modicum of the new. In fact, the author seems to regard modern morphologists as perhaps too narrow in their vision to possess the proper perspective for a general text. As a result, the two volumes now published are distinctly not up to date from the standpoint of modern morphology.

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[4] VELENOVSKÝ, JOS., Vergleichende Morphologie der Pflanzen. Vols. I and II. pp. 731. *pls. 5. figs. 455.* Prag: Fr. Řivnáč. 1905 and 1907.

The first volume (pp. 277), issued in 1905, is introduced by general discussions of questions that are not current in modern laboratories, however interesting they may have been during the domination of the Goethean morphology. The main part of the volume consists of "Die Morphologie der Kryptogamen." The illustrations are well selected and many of them are original. The ground has evidently been well traversed in the laboratory but not in recent literature, for the text gives a distinct impression of long isolation. Why do so many botanists fail to see the incongruity of such a series of names for coordinate groups as "A. Thallophyten," "B. Charophyta," "C. Moose," "D. Gefässkryptogamen"?

The second volume (pp. 454), issued in 1907, presents "Die Morphologie der Phanerogamen," in so far as the vegetative organs are concerned. The main divisions are "Die Keimpflanze," "Die Wurzel," "Das Blatt," "Die Achse," and "Die Trichome." The general attitude is indicated by the subdivisions under "Seedlings," which are as follows: seedlings of polycotyls, of monocotyls, of stemless plants, of acotylous plants.

The third volume is to contain the morphology of the "phanerogam flower" and a system of classification, besides a general index.

The work will undoubtedly prove a most interesting one for reference, especially for the younger generation of morphologists. —J. M. C.

MINOR NOTICES

North American Flora.—The first part of volume XXV has just appeared, being the fifth part published. It contains four of the sixteen families of Geraniales, the order with a synopsis of its families being presented by J. K. SMALL. The Geraniaceae, by L. T. HANKS and J. K. SMALL, contain four genera, a new genus *Robertiella* being founded on *Geranium Robertianum*. The species of Geranium number sixty-four, of which twenty-three are new, and Erodium and Pelargonium each contain six species. The Oxalidaceae, by J. K. SMALL, contain ten genera, *Hesperoxalis*, *Otoxalis*, and *Bolboxalis* being new and monotypic. The other genera are Oxalis (3 spp., 1 new), Ionoxalis (65 spp., 28 new), Monoxalis (2 spp., 1 new), Lotoxalis (11 spp., 1 new), Xanthoxalis (26 spp., 1 new), Biophytum (1 sp.), and Averrhoa (2 spp.). The Erythroxylaceae, by N. L. BRITTON, represented by the single genus Erythroxylon, contains twenty-eight species, one of which is new. The Linaceae, by J. K. SMALL, contain four genera, *Hesperolinon* being a new genus established on *Linum* § *Hesperolinon* Gray. The genera are Linum (5 spp.), Cathartolinum (48 spp., 10 new and all but one of the remainder transferred from Linum by SMALL), Hesperolinon (9 spp.), and Reinwardtia (1 sp.).—J. M. C.

Physiological pedagogy.—Though the notice is belated, a pamphlet by SCHLEICHERT,[5] illustrating the sort of instruction in plant behavior which he considers adapted to the eighth or ninth school year, deserves mention. The fundamental processes in germination, absorption, transpiration, photosynthesis, and respiration, are presented in simple fashion. There are appendices (1) giving a list of plants adapted for observation in the school garden; (2) on biological collections of plants; and (3) on simple methods (mostly devised by the author) for recognizing various plant stuffs.—C. R. B.

Diatoms of the Pacific.—MANN[6] has published the results of his investigation of the diatoms collected by the Albatross of the U. S. Bureau of Fisheries, during its fishery and deep-sea investigations in the Pacific in the years 1888–1904. The contribution contains a synoptical catalogue of the species, the data of the stations at which the diatoms were collected, and a very useful bibliography. The 51 genera recognized include 298 species, 41 of which are described as new. The large genera are Navicula (54), Coscinodiscus (34), and Biddulphia (30).—J. M. C.

Portraits of botanists.—The third and fourth parts of DÖRFLER'S series of portraits of botanists have been issued. A description of the general character of the series was given in this journal (**42**:496. 1906) upon the appearance of the first two parts. The third part contains the portraits of RUDBECK, LINNÉ (4), HALLER (2), SCOPOLI, JACQUIN, and ALLIONI; the fourth part, WULFEN, INGENHOUSZ, HEDWIG, GAERTNER, KÖLREUTER, SCHREBER, PALLAS, EHRHART, THUNBERG, and LAMARCK.—J. M. C.

Engler's Syllabus.—That the development of our knowledge of the relationships of plants is very rapid is evidenced by the appearance of the fifth edition of ENGLER'S *Syllabus*.[7] The most recent information about Cycadofilices was even so recent that it was inserted by means of a paster. It is a great boon to botanists that this publication keeps so well abreast of current knowledge, for it is a volume of daily consultation in every working laboratory.—J. M. C.

Flora of the Canadian Rockies.—Miss FARR[8] has brought together the plants of this interesting region collected by herself and reported by other botanists, and has presented a list of 763 species of vascular plants, 38 of which are pteridophytes, and 15 gymnosperms.—J. M. C.

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[5] SCHLEICHERT, F., Bieträge zur Methodik des botanischen Unterrichts (Sammlung Naturwissenschaftlich-pädagogischer Abhandlungen, Band **2**, Heft 3). Imp. 8vo. pp. iv+48. Leipzig and Berlin: B. G. Teubner. 1905. *M* 1.

[6] MANN, ALBERT, Report on the diatoms of the Albatross voyages in the Pacific Ocean, 1888–1904. Contrib. U. S. Nat. Herb. **10**:221–419. *pls. 44–54.* 1907.

[7] ENGLER, ADOLF, Syllabus der Pflanzenfamilien. pp. xxviii+248. Berlin: Gebrüder Borntraeger. 1907. *M* 4.40.

[8] FARR, EDITH M., Contributions to a catalogue of the flora of the Canadian Rocky Mountains and the Selkirk Range. Contrib. Bot. Lab. Univ. Penn. **3**:1–88. 1907.

NOTES FOR STUDENTS

Vegetation of the high Andes.—WEBERBAUER draws this picture of the andine vegetation:[8a] In the high Andes of central Peru most plants are not structurally xerophilous, and dessication by the high altitude is much restricted by the abundant precipitation and the prevalence of clouds. Were the danger of drying so great, one would expect that the moistest locations would bear the most species and the most vigorous forms, and that on the moist ground the vegetation would ascend higher than elsewhere. But the vegetation of the high Andes presents no such picture; the high-andine moor contains fewer species than the meadows of cushion and rosette plants, and none of those stouter forms which in their aspect recall the lower regions—the shrubs, tufted grasses, and tall-stemmed herbs; these grow by preference rather on the dry slopes, the stony ground, and the rocks; and upon a stony substratum the limits of vegetation run higher than upon well-watered ground. The explanation of these phenomena is to be sought, in my opinion, in the temperature of the ground. By the low temperature of the soil many plants are kept away from the moors, while the simultaneous high temperature of the rocks is favorable for vegetation. That temperature of the soil at these elevations plays an important rôle is indicated by the horizontal position of roots, referred to in an earlier paper,[8b] and by the very aspect of the vegetation.—C. R. B.

Transmission of tropistic stimulation.—FITTING[8c] has undertaken to ascertain in what manner the tissues of perception and reaction are connected that the stimulus indirectly determines the direction of the curvature. The work consists mainly of a study of phototropic response (coleoptile of the grasses, chiefly Avena) as affected by more or less complete disconnection of the tissue between the apex and base. Wounding by transverse incision or by splitting does result in a feeble traumatic response, but neither the growth nor the capacity for perception and response is significantly affected. It may be said that the reliability of the author's conclusions hinges largely upon the truth of this statement, but the reviewer finds no reason for doubt and the work of ROTHERT is in accordance with it. The author shows that whatever course transmission is compelled to follow, the curvature is entirely independent of the unilateral occupation of the perceptive organ by the stimulus. Individual segments of halved or quartered coleoptiles will respond if the segment includes a small portion of the apex. Even in leaves from whose central portion a large square of tissue has been removed, transmission occurs. The stimulation seems to spread with equal ease across or along the organ. The author regards it highly probable that phototropic transmission proceeds through the living substance. The paper maintains the high standard we have come to expect from this author.—Raymond H. Pond.

[8a] WEBERBAUER, A., Weitere Mitteilungen über Vegetation und Klima der Hochanden Perus. Engler's Bot. Jahrb. **39**:449–461. *pls. 4, 5.* 1907.

[8b] *Op. cit.* **37**:60 ff. 1905.

[8c] FITTING, HANS, Die Leitung tropistischer Reize in parallelotropen Pflanzenteilen. Jarhb. Wiss. Bot. **44**:197–253. *fig. 26.* 1907.

Ants and plants.—Ule has already smitten hard the theory of myrmecophily, according to which the complicated cavities and other structures have arisen by natural selection through the protection afforded by the symbiotic ants against injury by other ants and browsing animals. Now he concludes[9] that it must be given up almost entirely, because his more extended observations in the Amazon region, where such plants most do congregate, cannot be reconciled with the theory.

The ant plants grow most abundantly in flooded regions, where no leaf-cutting ants are found; the devastation by leaf-cutters is not so extensive as it has been reckoned by von Ihering; the weapons of the protective ants are not efficient, especially against thick-skinned animals, and are not capable of such wounds as those of many other ants; and the protection afforded, while possibly advantageous in the struggle for existence, is not sufficient to call forth the elaborate cavities and other "adaptive" structures. In explanation of the symbiosis, Ule would rather lay stress upon the initiative of the ants, which chose aptly the plants that suited their needs, and perhaps have modified them by the intimate and constant symbiosis, in much the same way as man has improved the wild ancestors of his useful plants. But the cavities must have *originated* through deeper-lying causes.

Ule adds a list of the ant plants found on his Amazon expedition, which includes 46 species in 11 families, the Melastomaceae having 17, and the Leguminosae and Moraceae each 7. He figures the extraordinary "tubers" (really Dischidia-like pitcher leaves) of *Polypodium bifrons* Hook., which serve as water sacs and incidentally as dwellings for *Azteca Traili*.

A still more vigorous objection is made by von Ihering,[10] who has studied the relations between *Cecropia adenopus* Mart. and its inhabitant, *Azteca Muelleri* Emery, in a much more thorough fashion than was done by Fritz Mueller and Schimper. He has given special attention to the life-history of the ants and the metamorphosis of their nests. The "Müllerian bodies," which grow on the leaf bases, are not used to feed the larvae but as food by the ants themselves, though they are by no means restricted thereto. The small tumors, produced from the inner parenchyma near the entrance to the hollow of the stem as a result of gnawing the prostoma open, contain sugary and fatty substances and serve as food. Von Ihering rejects absolutely the elaborate conceptions of "mutualism" and "myrmecophily," and declares in so many words that *Cecropia adenopus* can get along quite as well without ants as a dog can without fleas. He considers the ants mere parasites, completely adapted to this plant, without which they cannot prosper at all; but all the plant "adaptations" are like those that hosts everywhere show to parasites.—C. R. B.

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[9] Ule, E., Ameisenpflanzen. Engler's Bot. Jahrb. **37**:335–352. *pls. 5, 6.* 1906.

[10] Ihering, H. von, Die Cecropien und ihre Schutzameisen. Engler's Bot. Jahrb. **39**:666–714. *fig. 1. pls. 6–10.* 1907.

Regeneration and polarity.—In a paper which has escaped our attention until now (on account of the removal of Dr. McCallum to Arizona), Vöchting[11] takes up again these problems, stimulated by Klebs's report[12] of the surprising ease with which he was able to reverse the polarity of certain willows—the unattained goal of many a previous experimenter. Much of this paper is devoted to a reexamination of Klebs's work, which Vöchting is unable to confirm and against whose conclusions he enters vigorous protest. He finds no evidence that polarity has ever been reversed by any experimental condition; he still holds that it is a special property of the body, founded in the very structure of the egg, and that it is not induced (as Pfeffer thinks) by any external agent. This conclusion seems to be inevitable, when one observes the extremely different positions and conditions under which eggs develop into embryos. In regeneration the various natural or experimental conditions produce each an appropriate effect, according as they cooperate with or oppose or do not affect polarity. In a supplementary note, Vöchting expresses his complete agreement with the conclusions reached by McCallum.[13]

Miss Kupfer also attacks the problems of regeneration,[14] and after reporting in some detail her experimental work, concludes that polarity is less rigid than is generally believed, the "disposition to form roots being much more generalized . . . . and more easily energized than the power to form shoots;" and that regeneration is dependent upon an adequate supply of food.

Not satisfied because various theories of regeneration fail to account for the formation of one or another kind of organ "when each of the conditions previously ssigned as the causes of regeneration has been fulfilled," she proposes a modification of the *Stoff und Form* theory, postulating the existence of localized root-forming and shoot-forming enzymes. To this the same objections apply as to the older form of this theory; but the author has vague hopes that it may be capable of experimental test, though "no results ready for publication have as yet been obtained." One neglected assumption (also made by Goebel) needs quite as thorough investigation as any, namely, that food will accumulate at any point *before* growth begins.—C. R. B.

Ultramicroscopic structure.—Gaidukov continues his studies with the ultramicroscope, describing in a late paper[15] the appearances in starch grains, cell walls, and protoplasm.

After an introduction upon the principles involved in the various forms of the instrument, he reports that he could see in the starch grains concentric or excentric rows of particles, for which he uses NÄGELI'S term micellae. These are separated by spaces which are optically empty or possibly contain amicroscopic matter. On swelling, the micellae separate more and more and lose their regular arrangement. Cell membranes show an essentially similar structure, cellulose walls showing very small pale particles, woody and corky walls, on the contrary, having brilliant and large micellae.

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[11] Vöchting, H., Ueber Regeneration und Polarität bei höhern Pflanzen. Bot. Zeit. 64^1:101–148. *pls. 5–7.* 1906.

[12] Klebs, G. Willkürliche Entwicklungsänderungen bei Pflanzen 96 ff. Jena. 1903.

[13] McCallum, W. B., Regeneration in plants. Bot. Gazette 40:97–241. 1905.

[14] Kupfer, Elsie, Studies in plant regeneration. Mem. Torr. Bot. Club 12:195–241. *figs. 13.* 1907.

[15] Gaidukov, N., Ultramikroskopische Untersuchungen der Stärkekörner, Zellmembranen, und Protoplasten. Ber. Deutsch. Bot. Gesells.

Living cytoplasm is a hydrosol complex. The micellae show active Brownian movements, oscillation, wiggling, collision, recession, etc., even when actively streaming. The better nourished the cytoplasm is, the more numerous and closer are the micellae and the less the amplitude of the movements; and *vice versa*. By a thin hydrogel layer, a coagulum formed by the electrolytes present in the water of the cell wall and vacuole, this hydrosol is protected against further injury by coagulation or against excessive solution by water. The healing of this hydrogel layer or ectoplast after taking in or extruding solid particles (as in Amoeba) is explained as due to coagulation of the micellae of the hydrosol at the spot exposed by the break to the action of electrolytes. At the death of the protoplast there arises a hydrogel complex. The nucleus consists of a hydrosol complex poor in water. The chromatophores resemble rather the hydrogel complex. Microsomes consist of several micellae and are comparable to the *Micellarverbänden* of NÄGELI.

So far as these preliminary accounts show, GAIDUKOV is not merely reporting what he sees, but is making many assumptions as to their interpretation.—C. R. B.

Germination of fern and moss spores.—LAAGE[16] has made a somewhat extended study of the germination of fern and moss spores in darkness. By using both organic and inorganic solutions as culture media he was able to germinate *Osmunda regalis* and thirteen out of sixteen species of Polypodiaceae in darkness. Germination and starch formation were obtained in Osmunda grown in distilled water without the influence of light. Fe_2Cl_6 and $FeSO_4$ stimulated germination and cell division in Osmunda in darkness. Of all the Polypodiaceae, sown in darkness, *Pteris aquilina* and *Scolopendrium officinarum* germinated best, and *Asplenium lucidulum* and *Polypodium aureum* not at all. Contrary to the results of HEALD, higher temperatures were found to be detrimental to germination in the absence of light. No chlorophyll was produced in darkness, although reported by SCHILLING. The osmotic effect of the solutions on germinating spores was marked. Abnormal forms of rhizoids developed in distilled water cultures, and in 4 per cent. Knop's solution they were suppressed, while the young prothallia were deformed. A number of instructive tables showing the effect of solutions of different strengths on germination and number of cells produced in darkness are given. Of the mosses, Funaria and Bryum were germinated in darkness by using very attenuated solutions of inorganic salts as culture media. *Polytrichum commune* could neither be germinated in darkness in the solutions of inorganic salts nor by the addition of organic iron salts to the fluids. Moss spores have been germinated in darkness under chemical stimuli by both HEALD and TRÉBOUX. LAAGE is the first to report germination of fern spores by means of chemical stimuli.—W. J. G. LAND.

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[16] LAAGE, A., Bedingungen der Keimung von Farn- und Moossporen. Beih. Bot. Centralbl. 21:77–115. 1907.

Artificial apospory in ferns.—GOEBEL[17] has published the result of his studies on apospory in ferns and on regeneration in Vicia and Phaseolus. The main part of his paper is devoted to apospory and a very brief account is given of regeneration in Vicia.

Contrary to BOWER's statement that attempts to induce apospory, though successful in certain mosses, have been entirely without results in ferns, GOEBEL succeeded in inducing artificially aposporous prothallia from primary leaves of sporophytes in many forms among ferns, such as *Aneimia Drageana*, *Alsophila van Geertii*, *Ceratopteris thalictroides*, *Gymnogramme chrysophylla*, *Polypodium aureum*, *Pteris longifolia*, and others. On certain parts of the under surface, of margin or of petiole of the primary leaf, there are produced prothallia, sporophytes, or even structures which really seem to be intermediate between sporophyte and prothallium by their having stomata and antheridia.

GOEBEL drew three conclusions from his studies: (1) regeneration is more active in a young leaf than an older one; (2) the sporophytic structure is not the constant product of regeneration; (3) there seems to exist no great difference between the nuclei of prothallia and those of sporophytes, and accordingly no sharp distinction between the x and $2x$ generations. He adds, one might regard the prothallium, phylogenetically, as a rudimentary leaf bearing sexual organs, though to determine this question further investigation is necessary.

Among the three conclusions drawn by GOEBEL, the third is a great problem. He does not enter in his paper into nuclear detail at all; therefore, cytologically it is still an open question.—SHIGÉO YAMANOUCHI.

Items of taxonomic interest.—W. H. BLANCHARD (Torreya **7**:97–102. 1907), in discussing the eastern species of Amelanchier, describes 2 new species.—N. L. BRITTON (*idem* 102) has described a new Mexican species of Ribes.—H. D. HOUSE (*idem* 133–136), in a second paper on southern violets, has described a new species and a new hybrid.—W. H. BLANCHARD (*idem* 139, 140) has described a new Rubus (red raspberry) from Vermont.—E. BRAINERD (Rhodora **9**:93–98 1907) has begun a presentation of the older types of North American violets.—L. M. UNDERWOOD (Bull. Torr. Bot. Club **34**:243–262. 1907), in continuation of his studies on "American ferns," has published a preliminary review of the N. Am. Gleicheniaceae, all the species being referred to Dicranopteris, in which 18 species are recognized, 5 being described as new, and all the rest being transferred. —C. L. SHEAR (Bull. Torr. Bot. Club **34**:305–317. 1907) has described 21 new species of fungi, most of which were discovered during his studies of the fungous diseases of the cranberry. Three new genera are described: *Plagiorhabdus* (2 spp.), *Bothrodiscus,* and *Acanthorhynchus.*—O. STAPF (Jour. Linn. Soc. Bot. **38**:6–17. 1907) has established a new genus (*Hallieracantha*) of Acanthaceae, to include species from Borneo and the Philippines heretofore referred to Ptyssiglottis; 19 species are recognized, 11 of which are new.—R. LAUTERBORN (Ber. Deutsch. Bot. Gesells. **25**:238–242. 1907) has described a new genus (*Thioploca*) of sulfur bacteria, belonging to the Beggiatoaceae.—J. M. C.

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[17] GOEBEL, K., Experimentell-morphologische Mitteilungen: 1. Künstlich hervorgerufene Aposporie bei Farnen. 2. Ueber die Bedingungen der Wurzelregeneration bei einigen Pflanzen. Sitz. Kön. Bayer. Akad. Wiss. **37**:119–138. *figs. 13*. 1907.

The male gametophyte of the podocarps.—JEFFREY and CHRYSLER[18] have been able to examine the male gametophyte of certain species of Podocarpus and Dacrydium, as well as of Agathis, obtained from New Zealand and Java, so far as material preserved in alcohol or formalin would permit. The conspicuous feature is the development of a prothallial tissue, by division of the two original prothallial cells, consisting in some cases of as many as eight cells. The walls of this tissue break down and the nuclei are freed, even from their cytoplasm, and swarm into the pollen tube. The authors do not regard this as a primitive feature, but consider the "ground plan" of this development as indicating the derivation of the podocarps and araucarians from an ancestral stock allied to the Abietineae. This feature also indicates that the podocarps and araucarians may be more nearly allied than has been supposed.—J. M. C.

Infection experiments with mildew.—REED[19] has been investigating the question of "physiological species" among the mildews. Recent work on mildews has indicated that each genus, and often each species of host plant, has its own particular specialized form. Infection experiments were conducted with twenty-three different varieties of commonly cultivated cucurbits, representing five species and three genera (Cucurbita, Cucumis, and Lagenaria). Each of these hosts was readily infected when inoculated with the conidia taken from any other. There was no difference in the infecting power of the mildew on the different species and genera, and there is no evidence of any specialization in the mildew of the Cucurbitaceae.—J. M. C.

A lycopod with a seedlike structure.—Miss BENSON[20] has investigated the reproductive structures of BERTRAND'S *Miadesmia membranacea,* a herbaceous paleozoic lycopod. The megasporangium develops a single thin-walled spore, "which in development and structure resembles an embryo sac and germinates *in situ.*" The sporangium is surrounded by an integument with a small micropyle, which is surrounded by numerous long processes of the integument that "formed a collecting and incubating apparatus for the microspores." The "carpellary leaf" was shed at maturity and resembles a winged seed.—J. M. C.

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[18] JEFFREY, E. C., and CHRYSLER, M. A., The microgametophyte of the Podocarpineae. Amer. Nat. **41**:355–364. *figs.* 5. 1907.

[19] REED, GEORGE M., Infection experiments with the mildew on cucurbits, *Erysiphe cichoracearum* DC. Trans. Wis. Acad. Sci. **15**:527–547. 1907.

[20] BENSON, M., *Miadesmia membranacea* Bertrand; a new paleozoic lycopod with a seed-like structure. Abstract read before Roy. Soc. London, June 13, 1907.

The flowering plants of the Mesozoic.—In a recent address SCOTT[21] has brought together the recent discoveries among the Cycadophytes, especially those of WIELAND among the Bennettitales, and has seen in the structure of their strobili strong suggestions of angiospermous flowers. Such a connection would suggest the possibility that the angiosperms may have been derived from the Filicineae by a "short cut;" that the evolution of the angiospermous flower was a process of reduction; and that the presumption that the simplest angiospermous flowers are the most primitive is no longer tenable.—J. M. C.

The Taxoideae.—Miss ROBERTSON[22] has brought together the results of the recent researches among the Taxineae, with the view of reaching some conclusion as to the vexed question of phylogeny. She reaches the conclusion that the group has retained many relatively primitive characters, but has become considerably specialized; that it may be regarded as an offshoot from the Cordaitales, which in turn are derived from the Cycadofilices. The author also suggests that the "female flower" of Taxus "more closely recalls that of Cordaites than that of any other known plant."—J. M. C.

Embryology of Rhizophora.—COOK[23] has succeeded in securing some material for the study of the embryology of *R. Mangle.* Only one of the four ovules reaches the seed stage; the hypodermal archesporium cuts off two tapetal cells; the linear tetrad is probably formed; endosperm formation is abundant; the embryogeny is probably of the Capsella-type ; during the first growth of the cotyledons about one-third of the embryo and the greater part of the endosperm are thrust out of the sac and lie in the ovary cavity.—J. M. C.

Endemic species and mutation.—WILLIS,[24] in following up the suggestions of his work upon the flora of Mt. Ritigala,[25] has constructed an argument against the origin of species by natural selection and in favor of origin by mutation. He maintains that the evidence of the endemic species on Mt. Ritigala, of Ceylon in general, of Mauritius, and of New Zealand completely proves his position.—J. M. C.

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[21] SCOTT, D. H., The following plants of the Mesozoic age, in the light of recent discoveries. Jour. Roy. Micr. Soc. **1907**: 127–141. *pls. 6–9.*

[22] ROBERTSON, AGNES, The Taxoideae: A phylogenetic study. New Phytol. **6**:92–102. *pl. 1.* 1907.

[23] COOK, MELVILLE THURSTON, The embryology of *Rhizophora Mangle.* Bull. Torr. Bot. Club **34**:271–277. *pls. 22, 23.* 1907.

[24] WILLIS, J. C., Some evidence against the theory of the origin of species by natural selection of infinitesimal variations, and in favor of origin by mutation. Annals Roy. Bot. Gard. Peradeniya **4**:1–15. 1907.

[25] BOT. GAZETTE **43**:353. 1907.

NEWS

HOMER D. HOUSE has resigned the associate professorship of botany and bacteriology in Clemson College, S. C.

THOMAS D. EASON, a graduate of the Clemson Agricultural College, has accepted a position as assistant in botany at the North Carolina Agricultural College.

Dr. KARL GIESENHAGEN, assistant professor of botany in the University of Munich, has been appointed professor of botany in the Veterinary College at Munich.

THE ADDRESS of Professor FRANCIS E. LLOYD, director of the Department of Investigation, Continental-Mexican Division, Inter-continental Rubber Company, has been changed from Torreon, to Hacienda de Cedros, Mazapil, Zac., Mexico.

CANTERBURY COLLEGE, New Zealand, at the instigation of Professor L. COCKAYNE, has decided to establish a subalpine experimental station in the mountains, where the mountain flora of New Zealand can be studied under natural conditions. The site selected includes a virgin forest, about 300 acres in extent, of *Nothofagus cliffortioides.*

THE MACMILLAN COMPANY announce for publication in the autumn a practical textbook of plant pathology, by D. T. MACDOUGAL, F. S. EARLE, and H. M. RICHARDS; Notes of a botanist on the Amazon and Andes, by RICHARD SPRUCE, edited by ALFRED RUSSELL WALLACE; The physiology of plant production, by B. M. DUGGAR; Bacteria in relation to agriculture, by J. G. LIPMAN; and a new edition of MUIR and RITCHIE'S Manual of bacteriology.

THE GOVERNMENT of New Zealand has planned a magnetic, botanical, zoological, and geological survey of the Auckland and Campbell Islands, the expedition sailing early in November. The botanists will be as follows: L. COCKAYNE, ecologist; T. F. CHEESEMAN, floristic botanist; R. M. LANIG, algologist, and A. H. COCKAYNE, plant pathologist. The survey was first proposed and the details arranged by the Philosophical Institute of Canterbury, a branch of the New Zealand Institute.

THE NEXT MEETING of the American Association for the Advancement of Science will be held during Convocation Week, at the University of Chicago. The sessions of Section G will be held in the Hull Botanical Laboratory. Inasmuch as the Secretary of the Section is at too great a distance for quick mail service, it is particularly requested that titles of papers to be read be sent directly to Dr. HENRY C. COWLES, University of Chicago, Chicago, so that the Secretary, upon his arrival, may have all business promptly in hand.—F. E. LLOYD, *Secretary Section G.*

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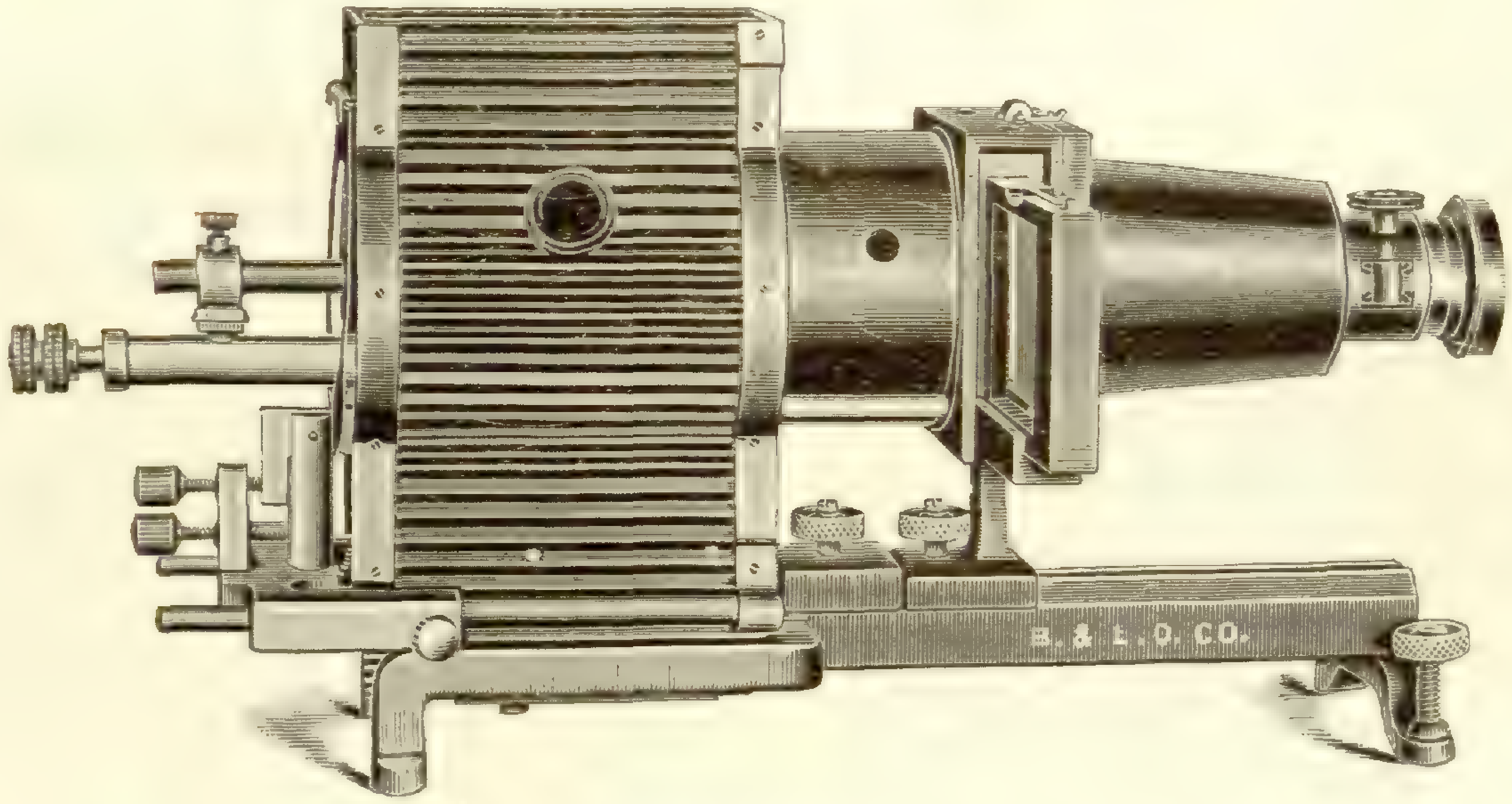

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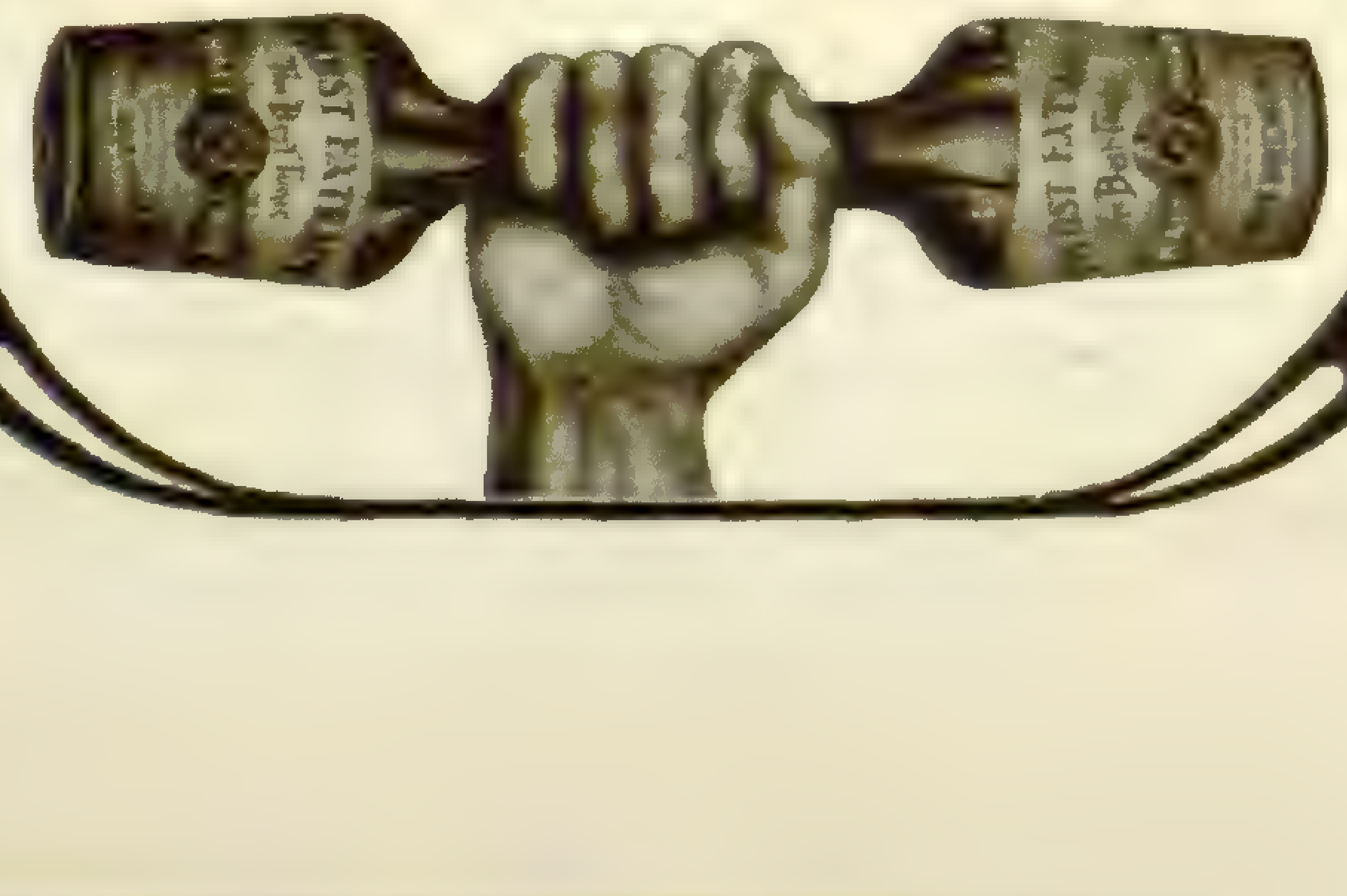

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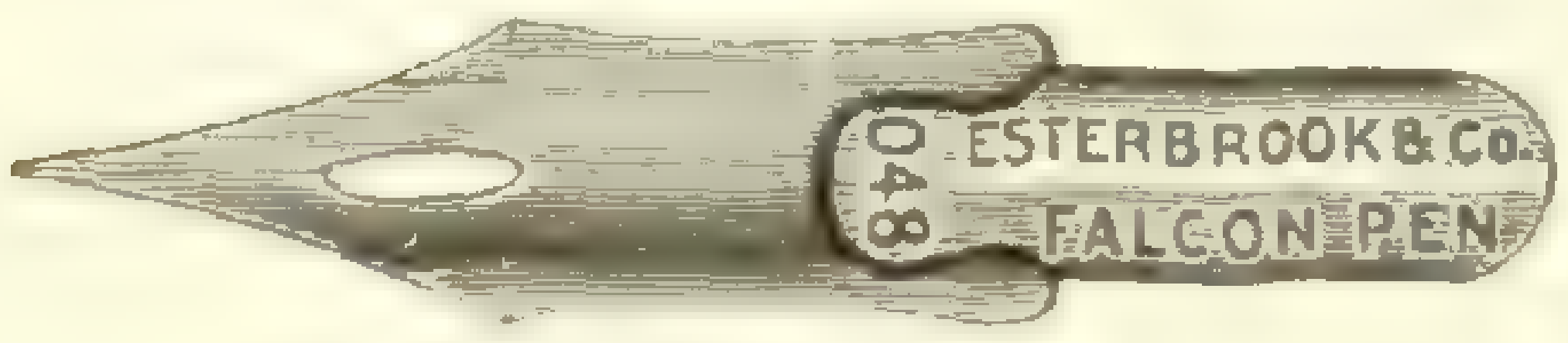

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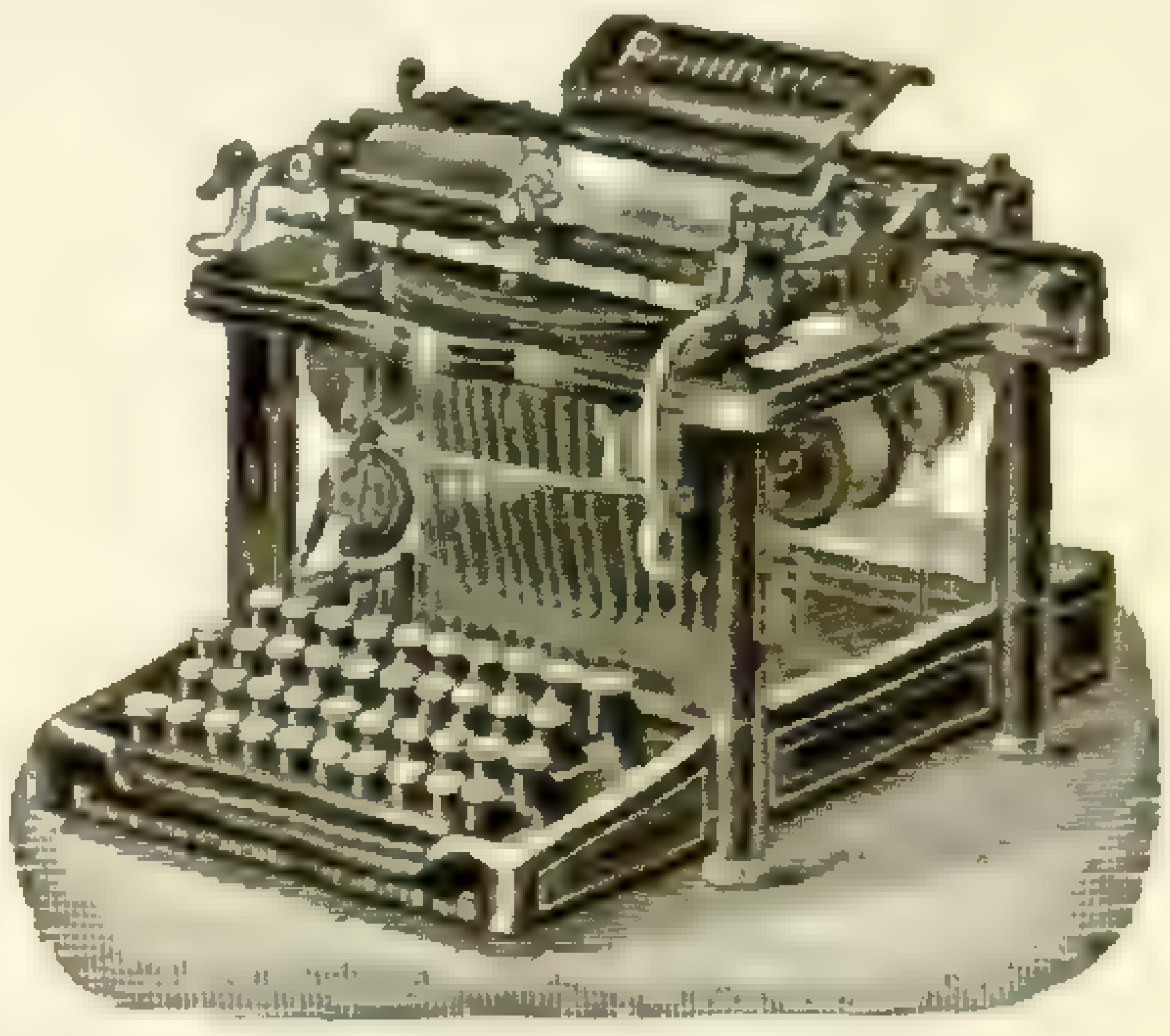

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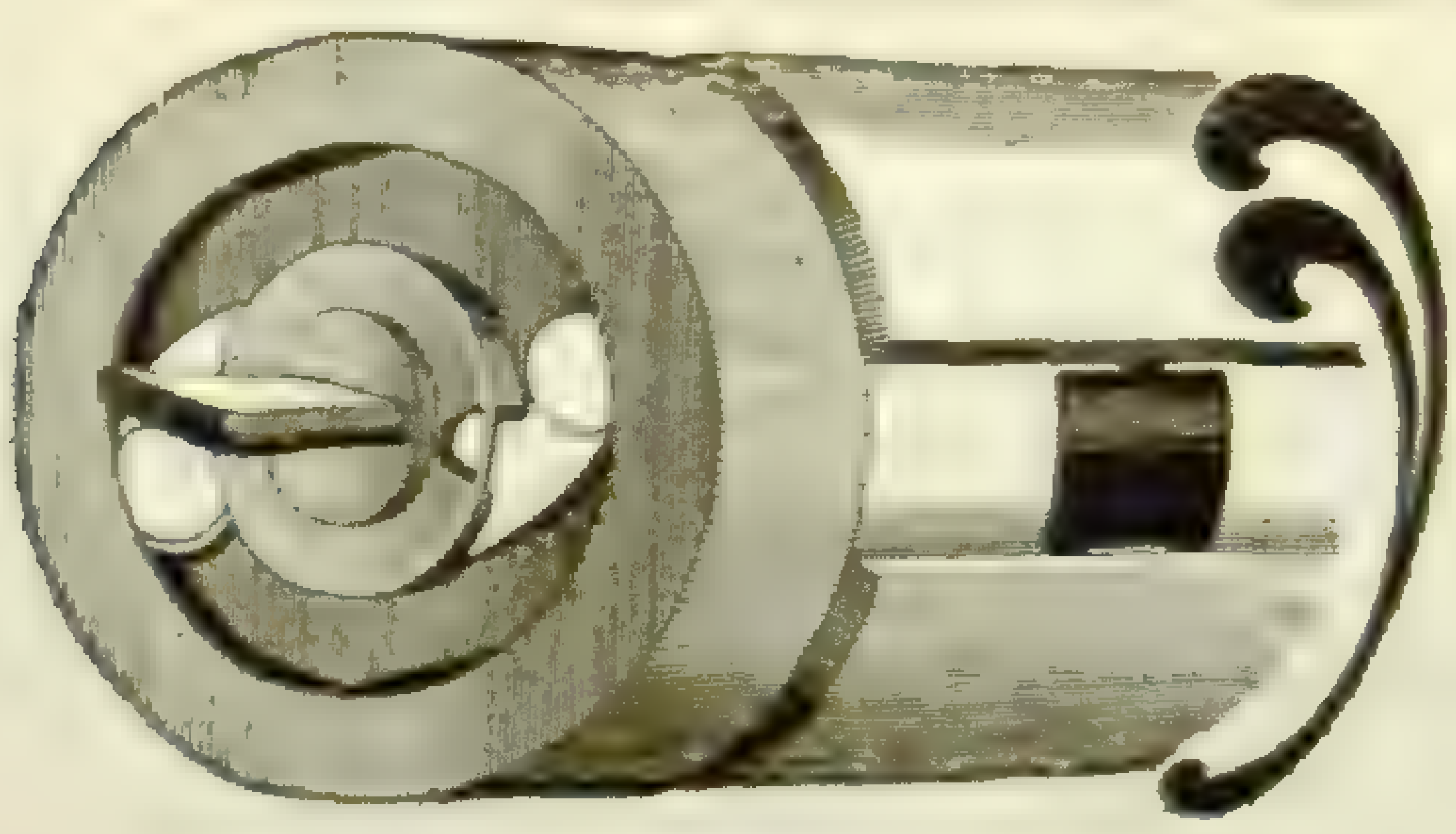

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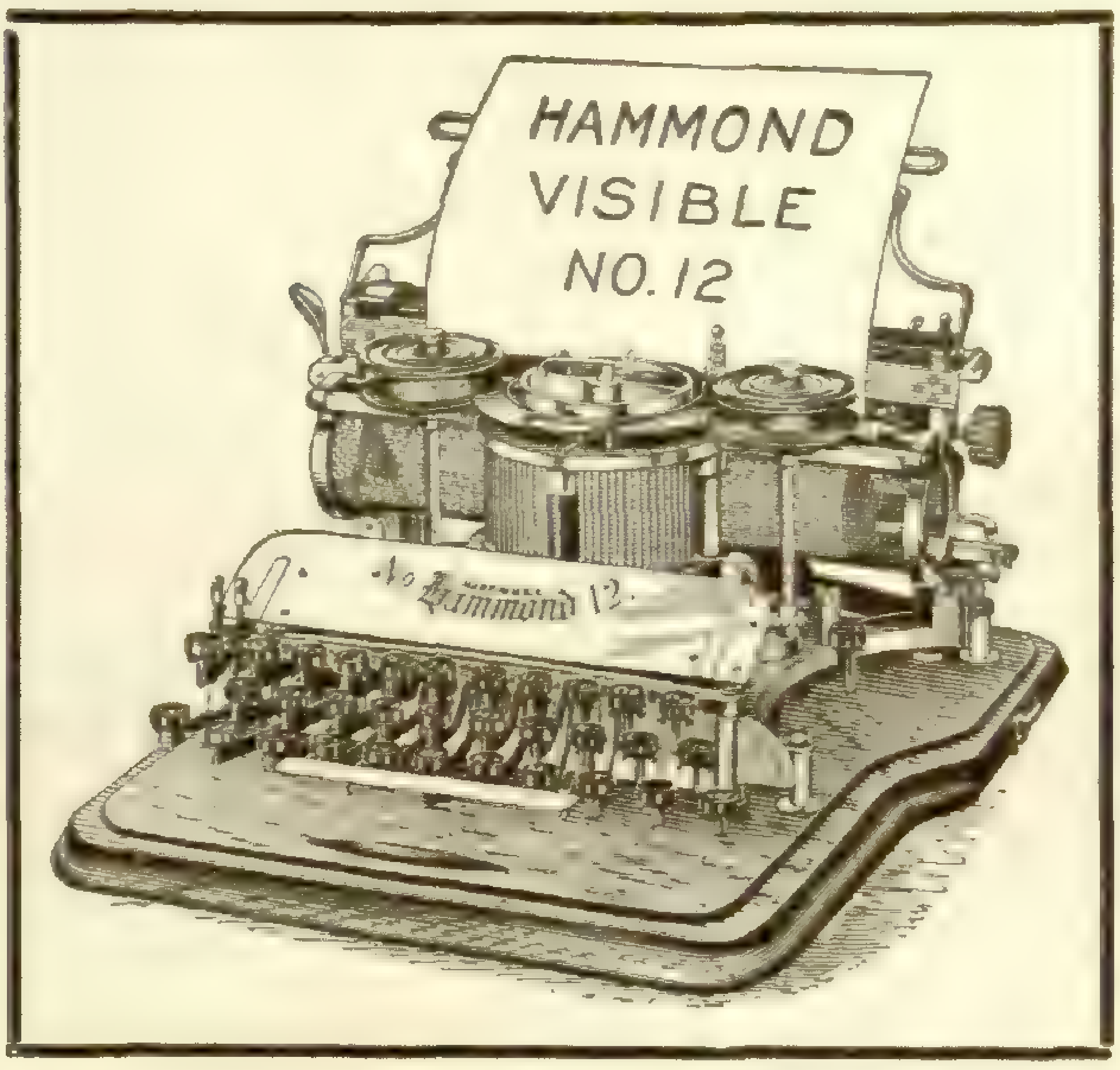

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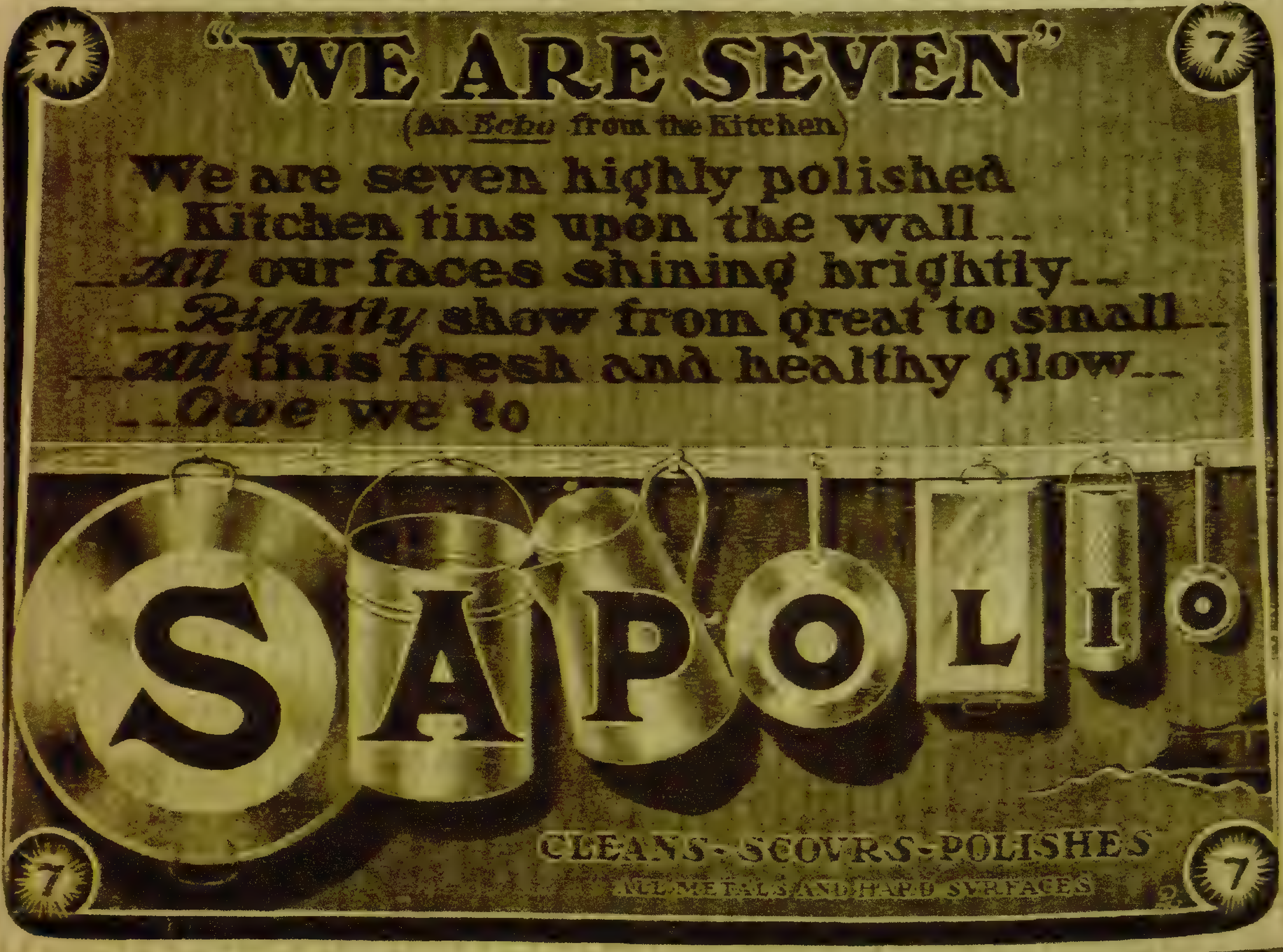
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THE
BOTANICAL GAZETTE

November 1907

Editors: JOHN M. COULTER and CHARLES R. BARNES

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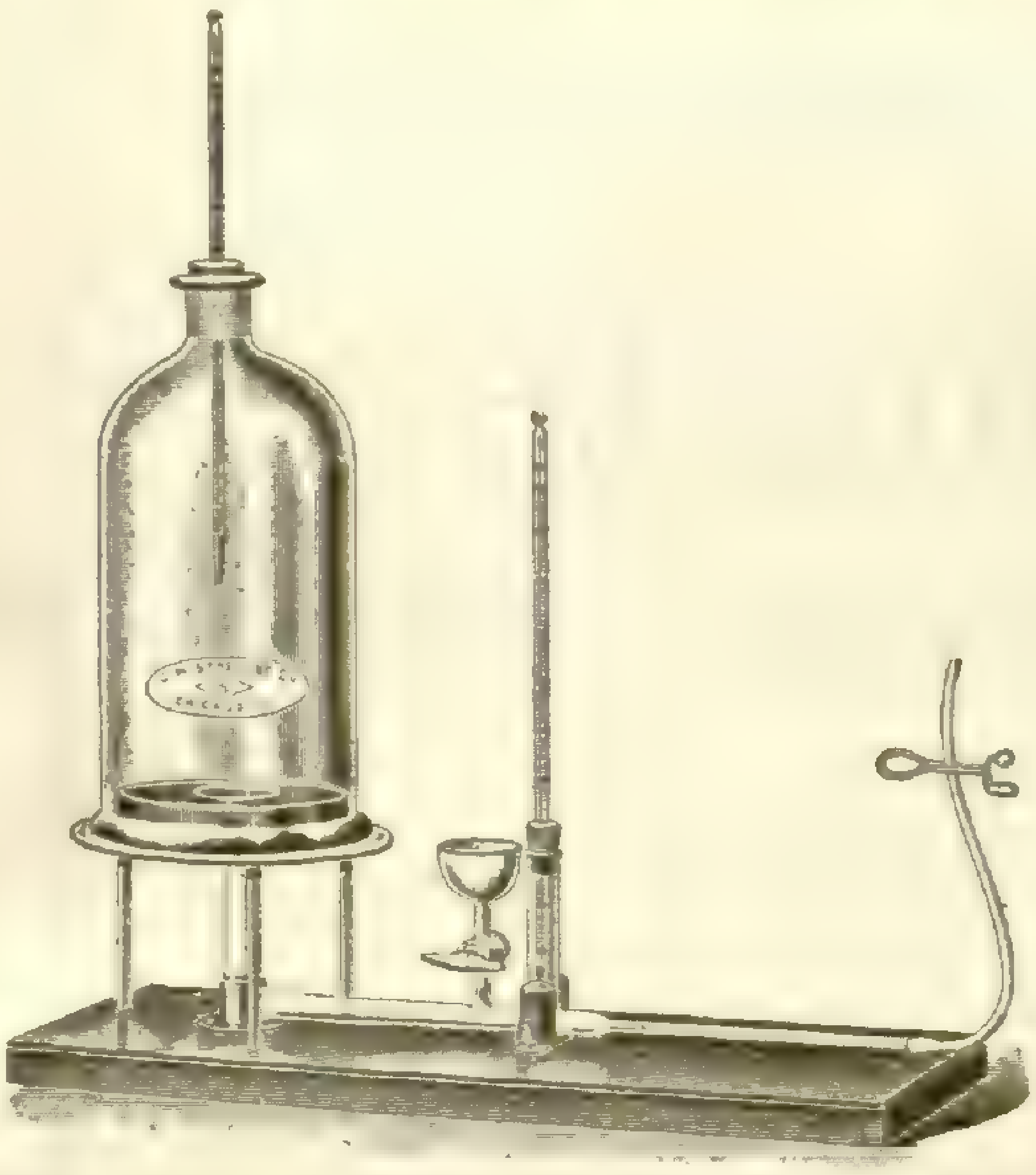

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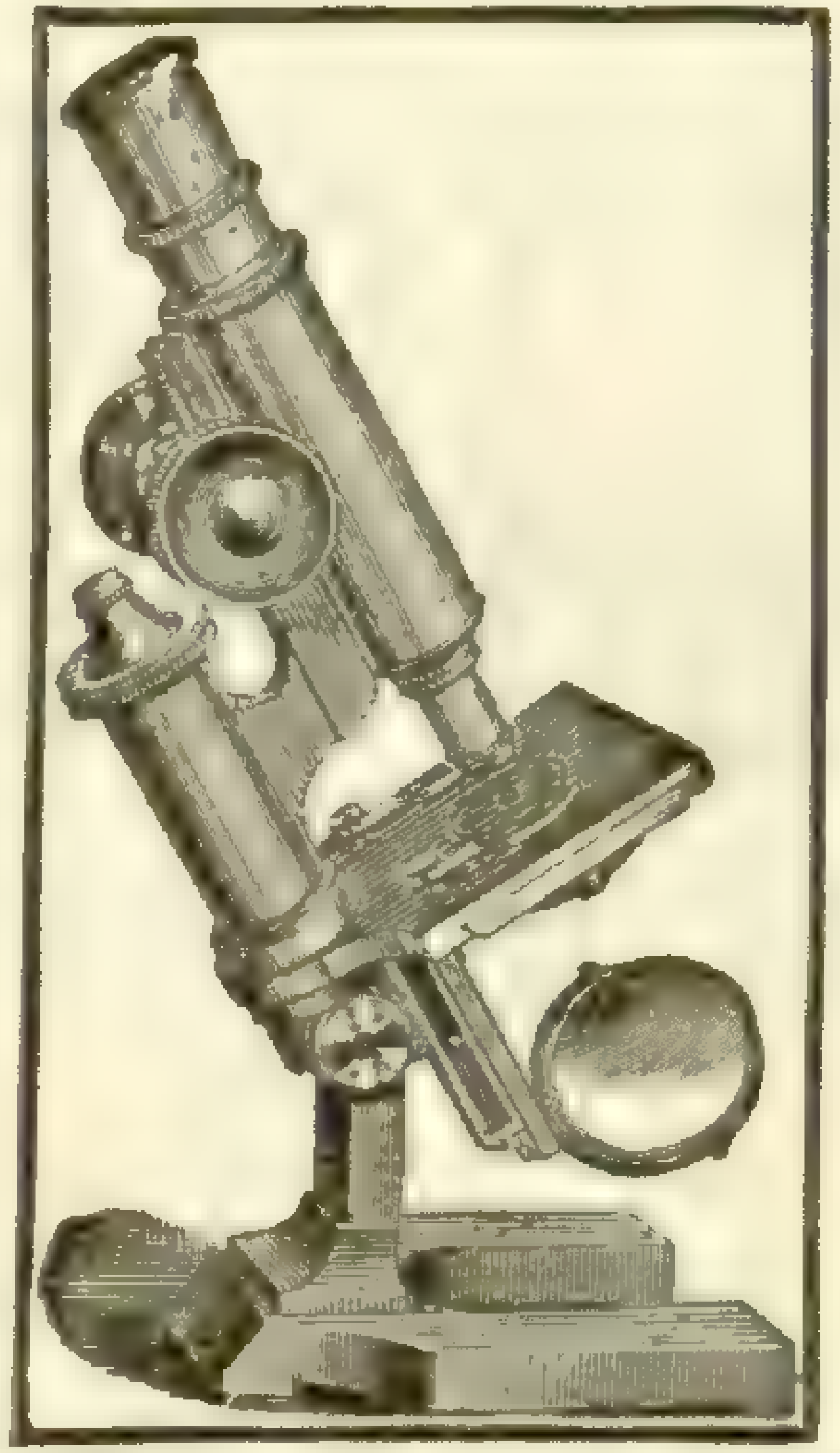

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VOLUME XLIV NUMBER 5

BOTANICAL GAZETTE

NOVEMBER 1907

THE FOREST FORMATIONS OF BOULDER COUNTY, COLORADO

ROBERT T. YOUNG

(WITH TWELVE FIGURES)

The present paper purposes to describe the forest formations of the eastern slope of the Rocky Mountains in Boulder County, Colorado. There has been a large amount of work done on the flora of Colorado from the systematic and distributional standpoint, the results of which are contained in RYDBERG'S *Flora of Colorado* (Bull. 100, Colorado Agricultural College Experiment Station, 1906). In the publications of the Forestry Bureau, U. S. Department of Agriculture, and the U. S. Geological Survey, there are a few papers treating of the economy (and incidentally the ecology) of the forests of the state; while a popular paper by RAMALEY ("Remarks on the distribution of plants in Colorado east of the divide") appeared in *Postelsia* for 1901, in which is given a considerable mass of data on the distribution and ecology of the plants of this region; but as yet there has been done no work of an exact character in the determination of the physical conditions under which the forests exist. For this reason I hope that the following discussion will prove of value.

The discussion will cover the following points: introduction, being a brief account of methods employed and a short description of the physical features of the region studied; composition of the forests with reference to the controlling and most common secondary species, and the relationship between them; physical character of the habitat with reference to water content of the soil, temperature of air and soil, humidity, light, pressure (altitude), slope, and exposure; past and present extent of the forests and their present movement, including deforestation and reforestation. The time spent in the investigations upon which this paper is based includes the summers of the years 1902 to 1905 inclusive.[1]

Introduction

The methods which I have employed are given in detail in a recent work, *Research methods in ecology*, by DR. F. E. CLEMENTS, and are therefore treated here very briefly. They include the use of a Draper psychrograph and thermograph, a geotome, aneroid barometer, maximum, minimum, and ordinary thermometers, egg-beater psychrometers, and a simple photometer.

A set of the Draper instruments was established in Boulder, at an altitude of 1620^{m}, and at timber-line on the east slope of the Continental Divide at an altitude of about 3420^{m}. A set of records of these instruments was taken between June 21 and July 20, 1905. The instruments were set each week by comparison with a watch and with the humidity and temperature readings obtained from the egg-beater psychrometer and the thermometer. The thermograph records were found to agree within a few degrees with the temperature as given by the thermometer, but very little confidence can be placed in the psychrograph records as the reading recorded by this instrument seldom, if ever, tallied with the readings given by the hand psychrometer, and in fact the two psychrographs when running side by side did not agree with each other closer than seven per cent.

A set of maximum and minimum thermometers was placed at the mouth of a small cañon at an altitude of 1710^{m} and readings taken weekly from June 23 to July 31, 1905. From August 4 to September 4 these were stationed on a moraine in open pine timber at an altitude of 2550^{m}. Another set was kept on the open plains three miles east of Boulder at 1590^{m} altitude from the middle of June to the end of September.[2]

With the geotome, two soil cores were obtained at each station, one of the first 11.25^{cm}, and one from 11.25 to 22.5^{cm} in depth.[3] These readings are of course not entirely satisfactory in determining the soil water available for the trees, with their roots extending to a depth of many feet; but the deeper sample probably

---

[1] See below.

[2] The thermographs and psychrographs were elevated about 1.2^{m} above the ground, the maximum and minimum thermometers 0.6^{m}. They were all carefully housed so as to protect them from the sun and yet afford free access to the air.

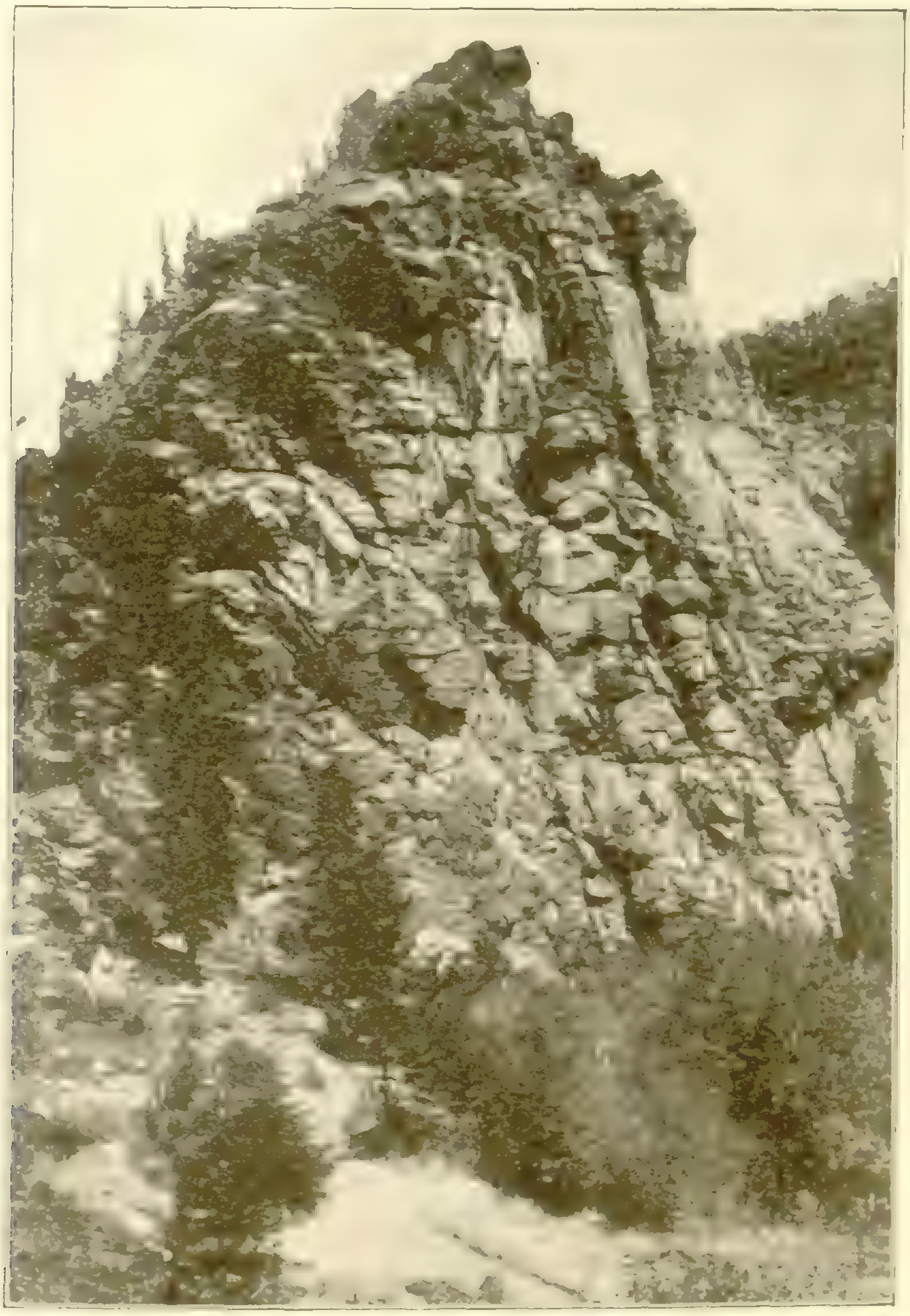

FIG. 1.—Castle Rock in Boulder Cañon, altitude 2250^m; in the foreground and to the right is seen the Populus angustifolia–Salix Nuttallii formation; scattered over the hills are Pseudotsugas and Piceas.

gives a fair basis for comparison of habitats in this respect. It is exceedingly difficult in any extended investigation to carry a geotome which will reach a depth of several feet. The soil samples obtained

[3] Exceptions to these depths will be noted below

with the geotome were carried to the laboratory in Boulder in tightly closed tin cans and weighed as soon as possible after collection. They were then opened, the samples dried for three days at an average temperature of 24 to 29°C., after which they were weighed again. The difference between the two readings gave the weight of moisture contained in the soil, and this weight is expressed in per cent. of weight of the dried sample. In the case of soil samples which it was necessary to carry in the pocket for several days before weighing, an allowance of a few decigrams must be made, since there was a slight evaporation from the tins. This slight inaccuracy, however, is not sufficient to invalidate the general results.

At each station soil temperatures were taken on the surface of the ground and at depths of 11.25^{cm} and 22.5^{cm}, respectively. The air temperature was taken at 7.5^{cm} and 9^{dm} above the ground; while humidity readings were also taken at 7.5^{cm} and 9^{dm} above the surface. Occasionally humidity and temperature readings at 1.8^{m} above the ground were taken.

The light readings in each formation were obtained with the photometer, and these were evaluated in terms of a standard series of ten readings of one to ten seconds respectively, taken at 12:30 P. M. on October 2 at 1620^{m} altitude in Boulder. A similar series was taken at noon on June 23, but unfortunately lost.

The aneroid barometer was used in obtaining the approximate altitudinal limits of the formations, and the altitudes so obtained were checked whenever possible by those obtained by the United States Geological Survey.

The observation stations were chosen at points as nearly typical as possible for each formation, and at most stations from three to many observations were taken during the summer of 1905.[4] Where the formations showed isolated societies within their limits, separate stations were selected for each of these.

Boulder County, Colorado, lies on either side of the fortieth parallel of north latitude. Its western boundary is the Continental Divide of the Rocky Mountains, while to the east it extends about 19^{km} from the base of the mountains. With the exception of the banks of streams on the plains, the forested area is confined to the mountains,

[4] Three observations were taken in 1907 as noted below.

which were originally pretty heavily timbered; but since the settlement of the region, the forests have been and still are disappearing. The topography of the mountains has been determined by vast elevation accompanied by extensive faulting, and followed by great erosion. The face of the country is exceedingly broken. High, rocky ridges alternate with deep cañons walled in by rocky precipices hundreds of feet in height, with an occasional granite dome isolated from the general mass. Such a dome is shown in *fig. 1*.

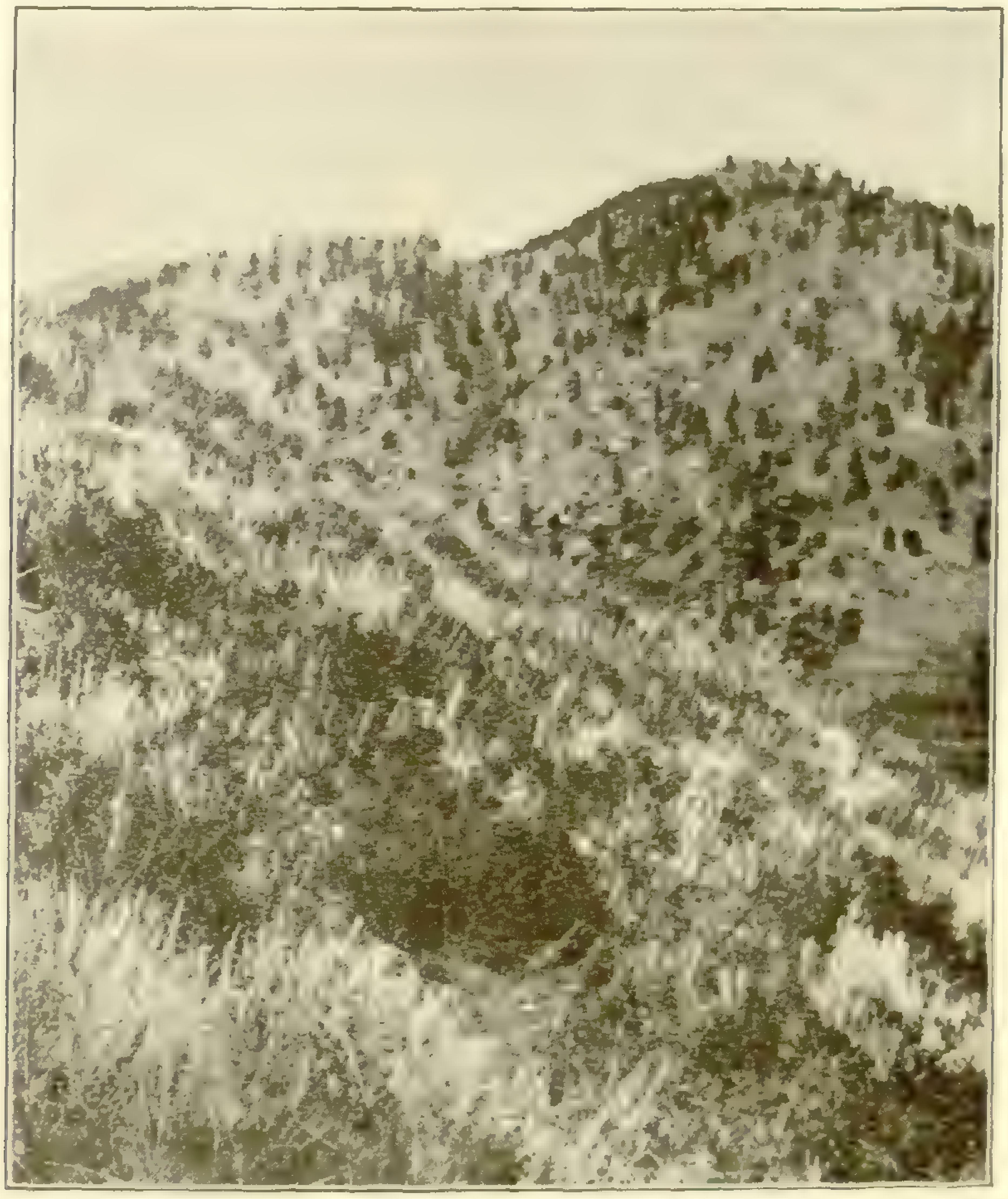

FIG. 2.—Foothills near Boulder; the altitude of the tops of the hills in the background is approximately 1950m; in the foreground is seen the shrub-grass formation of the foothills, which in this view is dominated by a grass-sagebrush society; scattered over the hills in the background is *Pinus scopulorum*.

Passing from the plains westward toward the Continental Divide, we first encounter the foothill region of the main range (*fig. 2*). This is a region of broken ridges with steep slopes, cut at intervals of 1.5

to 7^{km} by larger and smaller cañons running from east to west, in which flow the streams. Extending north and south from these main cañons are numerous smaller cañons and gulches, so that the entire region is very irregularly furrowed in all directions. The foothill region is 6 to 8^{km} wide and at its summit reaches an altitude of about 2250^{m}, although some of its individual peaks may reach a height of 2700^{m}.

From the western end of the foothills to the base of the main range is a distance of about 16^{km}. This is the plateau region, ascending gradually from 2250^{m} to 3000^{m} at the base of the range. While the surface of this region is much broken, it is less so than either the foothills to the east of it or the main range to the west, and its general contour is comparatively even. In its eastern part, however, where the streams lie far below the general level, are found the deepest and most rugged parts of the cañons. In its western portion are many beautiful little parks along the stream courses (*fig. 3*) which afford good crops of hay and excellent pasturage. Above 3000^{m} the country again becomes much broken, the steep and rocky slopes encountered above timber-line culminating at the crest of the range in vast chasms and inaccessible pinnacles of rock. Above 2400^{m} the mountains have been extensively glaciated. The ice sheet at the time of its greatest extent covered all but the highest ridges above 2700^{m}, while tongues of ice in some places extended down to nearly 2400^{m}. As evidence of this condition we have today the vast morainal deposits, the chains of little glacial lakes (*fig. 4*), and the existence of a small glacier on the eastern slope of the Arapahoe Peaks some 32^{km} west of Boulder. The highest summits in Boulder County are Mt. Audubon and the Arapahoe Peaks, with approximate altitudes of 4050^{m}.

The principal streams are North, Middle, and South Boulder Creeks, Jim Creek, the North and South St. Vrains, and Left Hand Creek. All of these rise at the base of the range and flow eastward to join finally the North Platte River.

The climate of the region is semi-arid. At Boulder, situated directly at the base of the mountains, the average rainfall for nine years has been 42.7^{cm}. In the higher mountains there is a much heavier annual rainfall than this, the difference between Boulder and the summit of the range being 25^{cm} in 1904. The rainfall at the base of the mountains occurs mainly in April and May, but in the higher mountains it is distributed through spring and summer.

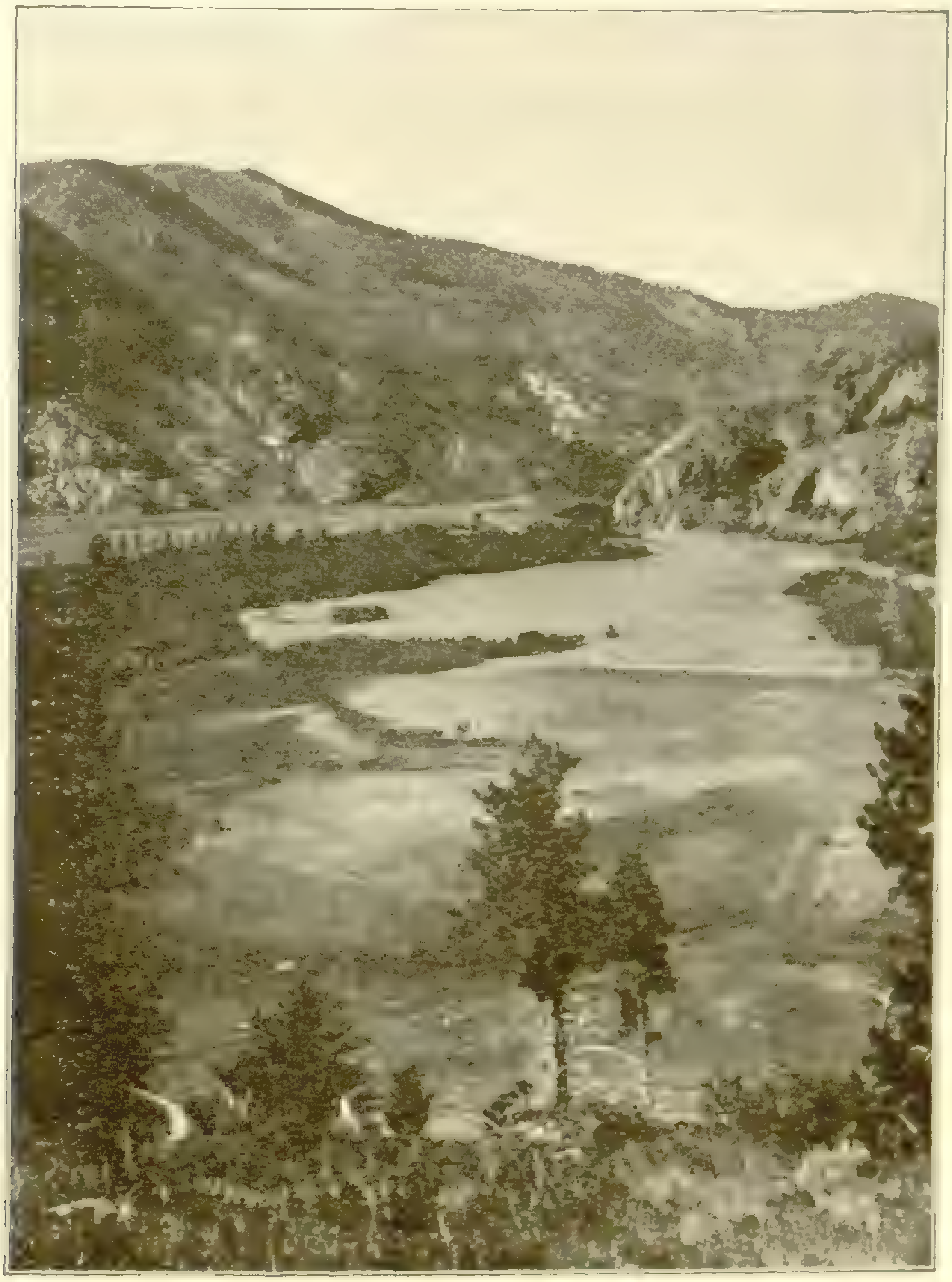

FIG. 3.—A mountain "park" on Boulder Creek, 35^{km} west of Boulder; in the foreground are a few *Pinus Murrayana* and *Pinus scopulorum*; in the middle foreground is the upper extension of the Populus angustifolia-Salix Nuttallii formation intermingled with *Populus tremuloides* and Piceas; to the right is an aspen grove; on the mountain in the background is a burned area in Pseudotsuga and *Pinus Murrayana* timber, in the lower part of which are a few aspen groves.

The heavy snows of winter, packed in the ravines by the high winds, do not melt until late in summer and are the principal source of water for irrigation.

At the base of the mountains the temperature range is from 37°7 to −34°4, though neither of these figures is often reached by thermometers elevated a few feet above the surface of the ground.[5]

The following is the record of maximum and minimum temperatures obtained by me during the summer of 1905: At Boulder (1620^{m}) from June 21 to July 20 the maximum thermograph reading was 34°4, the minimum 5°. At timber-line during the same period the maximum thermograph reading was 22°2 and the minimum −3°9. Three miles east of Boulder on the plains (1590^{m}) the maximum and minimum thermometers from June 13 to July 31 gave a maximum of 40°3 and a minimum of 6°1; from July 31 to August 31 a maximum of 41° and a minimum of 9°7.[6] The instruments at the cañon mouth (1710^{m}) from June 13 to July 31 gave a maximum of 31° and a minimum of 7°7, while those on a moraine (2550^{m}) from August 1 to August 29 gave a maximum of 30°3 and a minimum of 4°7. These results show an approximate difference in mean temperature of 11° between Boulder and timber-line, an approximate difference of 1° per 160^{m} altitude, the difference in the maxima being slightly greater and in the minima slightly less than this. It must of course be borne in mind in the study of these results that they are fragmentary, covering comparatively short periods.

As already remarked, comparatively little confidence can be placed in the psychrograph records. The curves traced by the two instruments are in no way conformable to each other, owing to the fact that the relative humidity is dependent on such local factors as sunlight and wind and hence is liable to sudden and considerable variations within limited areas. I have even known the temperature recorded by the wet-bulb thermometer to fall 1°5 C. within a few seconds when a sudden breeze sprang up, succeeding a calm. These facts show that a comparison of humidity readings between different stations at any given instant of time is open to serious error, and even the readings of the dry-bulb thermometer may vary locally owing to local conditions.

In the following discussion I shall consider a "formation" as a group of plants of definite composition as to species, occupying a definite habitat as to the physical characteristics of the latter, or a definite area as to geographical position. A "society" is a definite group of plants as to component species occupying a secondary position within a formation. The "characteristic species" of a formation are those which dominate the area occupied by that formation. Thus the "characteristic species" of the "cottonwood-willow formation" of the lower cañons and plains are *Populus occidentalis* and *Salix fluviatilis*. Within this "formation" we find the Crataegus and Corylus "societies."[7]

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[5] All temperatures are recorded in degrees Centigrade.

[6] The great difference between the maximum at Boulder and three miles east of Boulder is doubtless traceable to the different elevations of the instruments above the ground at these points.

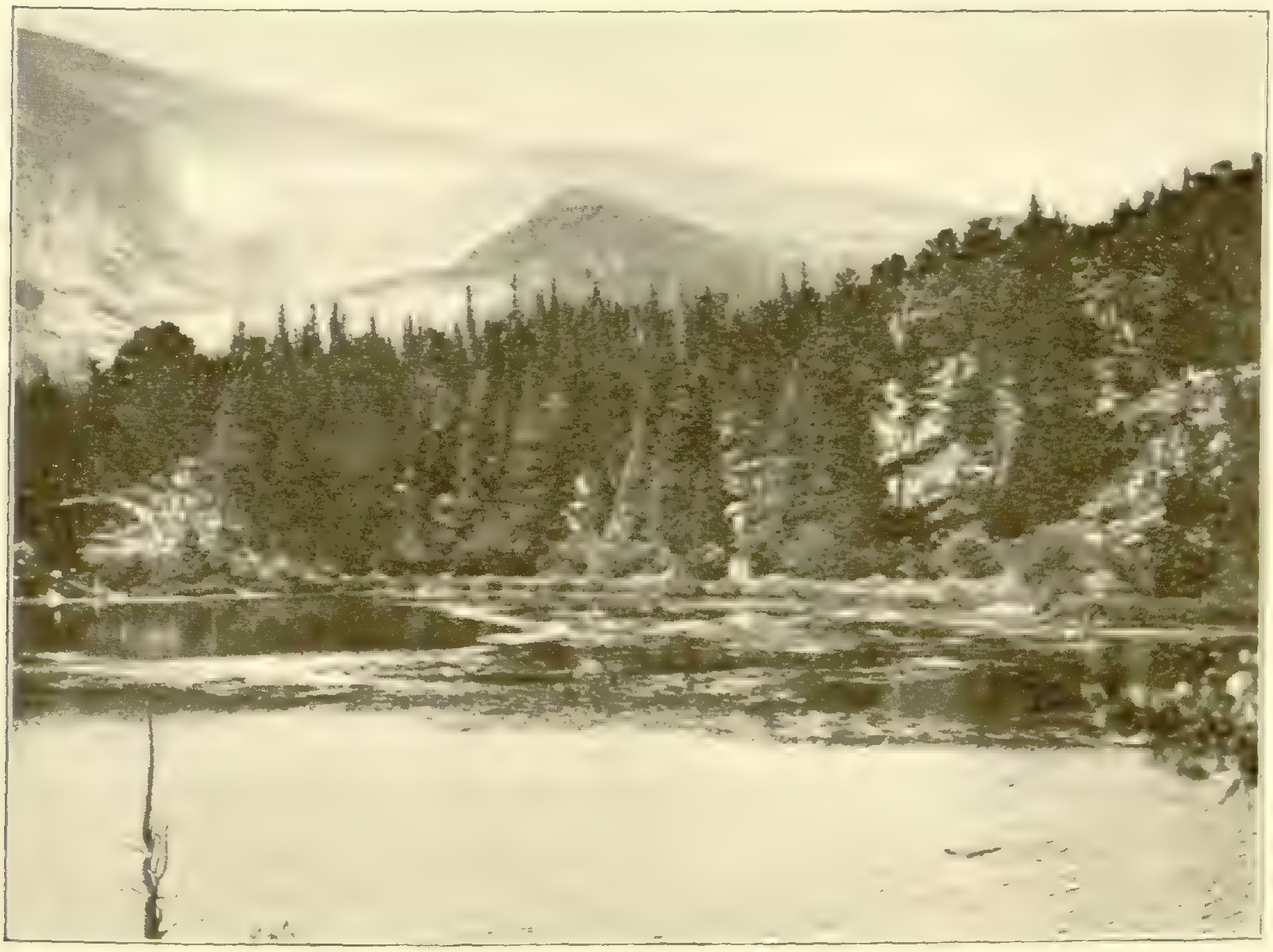

FIG. 4.—The Picea-Abies formation with a glacial pond in middle foreground.

Composition of the forests

The forests of Boulder County may be classed under the following formations: (1) Populus occidentalis–Salix fluviatilis formation; (2) Populus angustifolia–Salix Nuttallii formation; (3) Pinus scopulorum formation; (4) Pinus Murrayana formation; (5) Apinus flexilis formation; (6) Pseudotsuga–Picea Engelmanni formation; (7) Picea Engelmanni–Abies lasiocarpa formation.

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[7] I have given these definitions for the sake of clearness, but with no claim of originality. The nomenclature of the paper is that used by RYDBERG (*op. cit.*).

While *Populus tremuloides* occupies numerous areas through the mountains, I have not thought best to consider it of higher rank than a society. My reason for denying it formational rank is that it occupies varying habitats, associating with the other formations, and never dominating areas which are well defined either as to their physical features or geographical position.

All these formations are montane excepting the first, and even this extends up the cañons to about 1950^m. The second, on the contrary, while chiefly montane, overlaps the first on the plains.

(1) THE POPULUS OCCIDENTALIS–SALIX FLUVIATILIS FORMATION (*fig.12*)

This formation occupies the banks of streams on the plains and, as already mentioned, is found also in the lower cañons. It is a straggling tree formation scarcely worthy the name of forest. While restricted mainly to the stream banks, groves of trees may occasionally be found along the borders of the old flood plains.

It is a very mixed formation, consisting essentially of two layers, an upper woody layer and a lower herbaceous one. The former may be divided into two subordinate layers, one controlled by *Populus occidentalis* and the other by *Salix fluviatilis*. These are not, however, usually coexistent, but alternate, the cottonwood controlling here and the willows there. Associated with the two characteristic species of the formation are many individuals of *Populus angustifolia*, but these do not control. A few scattered shrubs occur in the formation but are not sufficiently numerous to be considered as an independent layer (see below). The herbaceous layer, moreover, might be separated into two subordinate ones; but since its constituent forms present every gradation in height, such a separation would be entirely arbitrary and superficial. A ground layer of mosses and liverworts is occasionally present.

The formation is an open one. Occasionally the trees form a sufficiently dense growth to exclude all but the more shade-loving species, but for the most part they are separated by intervals of many feet, thus permitting the entrance of a large amount of sunlight and admitting most of the species from the adjoining formations. These species are largely ruderal, owing to the presence of cattle and the proximity of farms and highways.

Of the weeds entering into the formation some of the commonest are *Medicago sativa*, *Melilotus alba*, *M. officinalis*, *Trifolium pratense*, *T. repens*, *Phleum pratense*, *Poa pratense*, *Bromus brizaeformis*, *Polygonum lapathifolium*, *Verbascum thapsus*, *Ambrosia trifida*, *Solidago canadensis*, and *Helianthus grosseserratus* (?).

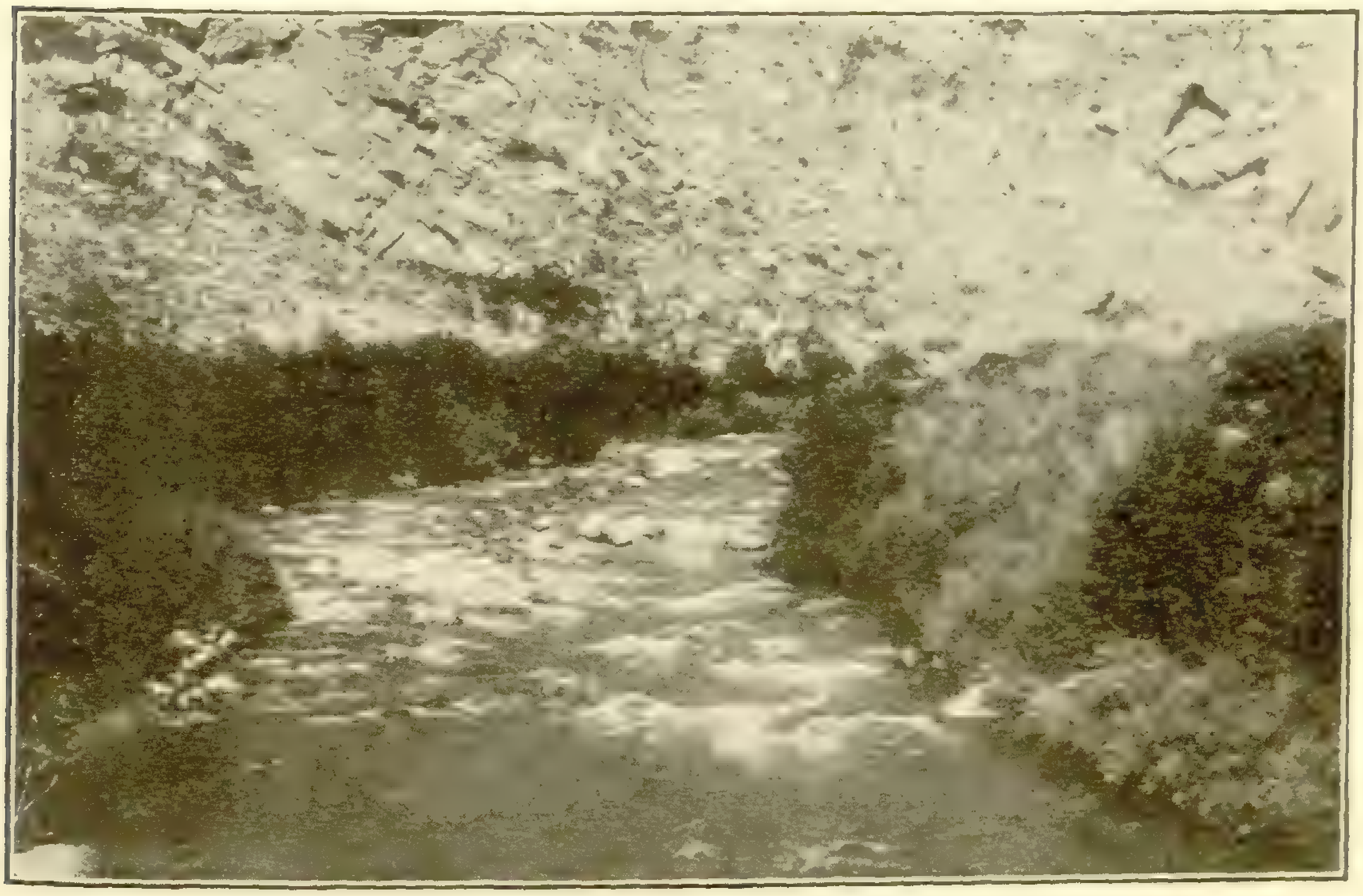

FIG. 5.—The Populus occidentalis–Salix fluviatilis formation, two miles above the mouth of Boulder Cañon; to the left the control is shared by *Populus occidentalis* and *Rulac negundo;* to the right *Salix fluviatilis* dominates.

In the more dense parts of the formation, the forms of the under layer are more sparse both as to number of species and number of individuals. Three of the more characteristic are *Anemone canadensis*, *Vagnera stellata*, and *Viola canadensis*.

The stream banks form a path along which some of the montane species are invading the plains. Hence we find in the cottonwood formation a few such forms as *Viola canadensis* and *Apocynum* *androsaemifolium*. A few species from the adjoining plains are invading the formation. These include an occasional *Artemisia* sp. and a few individuals of *Festuca octoflora*. *Eleocharis palustris* wanders in occasionally from nearby meadows.

While the under layer of the formation is so mixed that it is difficult to assign a dominant rôle to any forms, yet in general it may be said that this layer is characterized by *Agrostis alba* and *Melilotus alba*. The vernal aspect is not derived from any species or group of species, the color of the vegetation at this season being mainly green. In its late aestival and autumnal aspect the yellow of Solidago and Helianthus gives to the vegetation its predominant color.

In the lower cañons (*fig. 5*) the formation maintains the loose straggling character which it presents on the plains. Here, however, an intermediate layer of shrubs forms one of the most important parts of the formation (*figs. 5, 6*). Chief among these are *Alnus tenuifolia* and *Corylus rostrata*. Other members of this layer are *Crataegus cerronis*, *C. coloradoensis*, *Clematis ligusticifolia*, *Ampelopsis pentafolia*, *Prunus americana*, *P. melanocarpa*, *Rosa pratincola*, and *Acer glabrum*. In the densely shaded thickets formed by these shrubs, the under layer is composed mainly of *Hydrophyllum Fendleri*, *Viola canadensis*, *Galium trifidum*, and *Vagnera stellata*. Species from the higher slopes occasionally wander in, such as *Berberis Fendleri* and *Prunus melanocarpa*.

In places where the light value falls as low as 5 : 300, the under layer is largely lacking.

Mixed as is this formation on the plains, in the narrow and steep-sloped cañons its continuity is still more difficult to follow. The species from the adjoining shrub-grass formation of the cañon sides come down to the bottom of the cañon and mingle with those of the cottonwood-willow formation, ruderals are numerous, and along the stream banks members of the brookside formation, such as *Collinsia parviflora*, *Mimulus minor*, and *Veronica peregrina*, are found. Wherever sandbars are formed by the shifting current of the streams on the plains, the cottonwoods, principally *Populus occidentalis*, are invading them in large numbers. Such invasions, for the most part, are only temporary, however, on account of the floods which in spring overflow these sandbars, destroying the plants on them.

Owing to the physical condition of the surrounding habitats, the Populus occidentalis–Salix fluviatilis formation is in a practically static condition. My data on the physical characters of the habitat of this formation are as follows:

Observations taken on Boulder Creek east of Boulder during July 1905 gave results as follows:

*Temperatures**

(Observations July 3, 11 A. M.; 10, 10:45 A. M.; 24, 11:15 A. M.; 28, 1:45 P. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+9^{dm}$
Minima......	16°.2	16°	16°.6	20°.5	21°.2
Maxima......	20°.25	18°.5	31°.25	26°.5	25°.5

*Zero indicates the ground surface, minus readings below surface, and plus readings above the surface.

Water content

Observations	11.25^{cm}	$22.5-11.25^{cm}$
July 10......	30.1 per cent.	18.3 per cent.
July 24......	8.8 per cent.	9 per cent.

Relative humidity

(Observations July 3, 11 A. M.; 10, 10:45 A. M.; 24, 11:15 A. M.; 28, 1:45 P. M.)

	7.5^{cm}	9^{dm}
Minima......	43 per cent.	38 per cent.
Maxima......	73 per cent.	60 per cent.

The light value in this formation taken above the under layer at noon on August 7 was 9 : 180.

In a thicket of *Corylus rostrata* at the mouth of Boulder Cañon, three series of observations gave the following results:

Temperatures

(Observations June 24, 10:15 A. M.; July 17, 12:20 P. M.; August 30, 7 A. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+8^{dm}$	$+1.8^{m}$
Minima......	13°.5	13°.8	14°.4	16°.75	17°	17°.5
Maxima......	18°	18°	21°.5	25°.5	27°	27°.5

Water content

Observations	11.75^{cm}	$22.5-11.25^{cm}$
June 24......	29.5 per cent.	24.6 per cent.
July 17......	12.5 per cent.	12.4 per cent.
Aug. 30......	5.3 per cent.	7.2 per cent.

Relative humidity

(Observations June 24, 10:15 A. M.; July 17, 12:20 P. M.; August 30, 7 A. M.)

	7.5^{cm}	9^{dm}	1.8^{m}
Minima........	30 per cent.	27 per cent.	26 per cent.
Maxima........	80 per cent.	83 per cent.	88 per cent.

In a hawthorn society at the mouth of a small cañon at an altitude of 1710^{m}, observations were made at three stations. One of these was in the center of the thicket, close to a small stream; this I shall designate as Station E. A second station, which I have called E_1, was chosen about midway between the center and edge of the thicket; and the third, or Station E_2, was taken just at the edge of the thicket. The results obtained for these three stations follow:

Temperatures

Station E (Observations June 12, 7 P.M.; 13, 6 P.M.; July 1, 8:15 A.M.; 8, 10:30 A.M.; 17, 9:10 A.M.; August 26, 9:45 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}	+7.5^{cm}	+9^{dm}	+1.8^{m}
Minima......	14°.2	13°	14°	12°*	12° †	16° †
Maxima......	19°	20°.75	25°	26°.5*	26°.5 †	28° †

* Five observations.

† Four observations.

Station E_1 (Observations June 13, 6 P.M.; July 1, 8:45 A.M.; 8, 11 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}
Minima................	13°.6	13°.4	13°
Maxima................	15°.2	15°.5	16°.8

Station E_2 (Observations June 13, 7 P.M.; July 1, 9:15 A.M.; 8, 11:15 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}
Minima................	14°.75	15°	14°.6
Maxima................	17°.6	17°	19°.5

Water content

	Observations	11.25^{cm}	22.5−11.25^{cm}
Station E.......	June 14	22.8 per cent.	30.8 per cent.
	July 1	25.3 per cent.	33.3 per cent.
	July 8 (raining)	25.8 per cent.	35.6 per cent.
	July 17	11 per cent.	16.7 per cent.
	August 26	6.2 per cent.	9.6 per cent.
Station E_1......	July 1	14.4 per cent.	15.4 per cent.
	July 8 (raining)	18.6 per cent.	13.3 per cent.
Station E_2......	July 1	6.2 per cent.	13.3 per cent.
	July 8 (raining)	10.2 per cent.	16.3 per cent.

Relative humidity

Station E (Observations. June 12, 7 P.M.; 13, 6 P.M.; July 1, 8:15 A.M.; 8, 10:30 A.M.; 17, 9:10 A.M.; August 26, 9:45 A.M.)

	7.5^{cm}	9^{dm}	1.8^{m}
Minima........	45 per cent.	42 per cent.	21 per cent.
Maxima........	80 per cent.	77 per cent.	77 per cent.

Light value

Station E...............	August 26	9:45 A. M. = 5: 300

(2) THE POPULUS ANGUSTIFOLIA–SALIX NUTTALLII FORMATION (*fig. 1*)

The transition between this and the preceding formation is a wholly gradual one, the narrow-leaf cottonwood occurring, as already noted, as a secondary form in the preceding formation. The upper limit of *Populus occidentalis* is about 1950m. At this altitude it is replaced by *Populus angustifolia*.

Like the preceding, this formation lacks continuity, the characteristic species only occasionally exercising control, and being interrupted in places by the Pseudotsuga-Picea formation. In scattered association with *Populus angustifolia* and *Salix Nuttallii* are *Alnus tenuifolia*, *Betula fontinalis*, *Acer glabrum*, and in the lower parts of the mountains an occasional *Salix Fendleriana*. These shrubs form a straggling society along the cañon bottoms and may be occasionally found running up the mountain sides in favored localities. Two under layers, one of flowering plants, the other of mosses, liverworts, and lichens, are usually present; but these layers, as well as the upper, lack continuity and are very open. The herbaceous, or middle layer, is very mixed and holds no definite level, owing to the varying height of its constituent species. The frequent presence of a highway in the

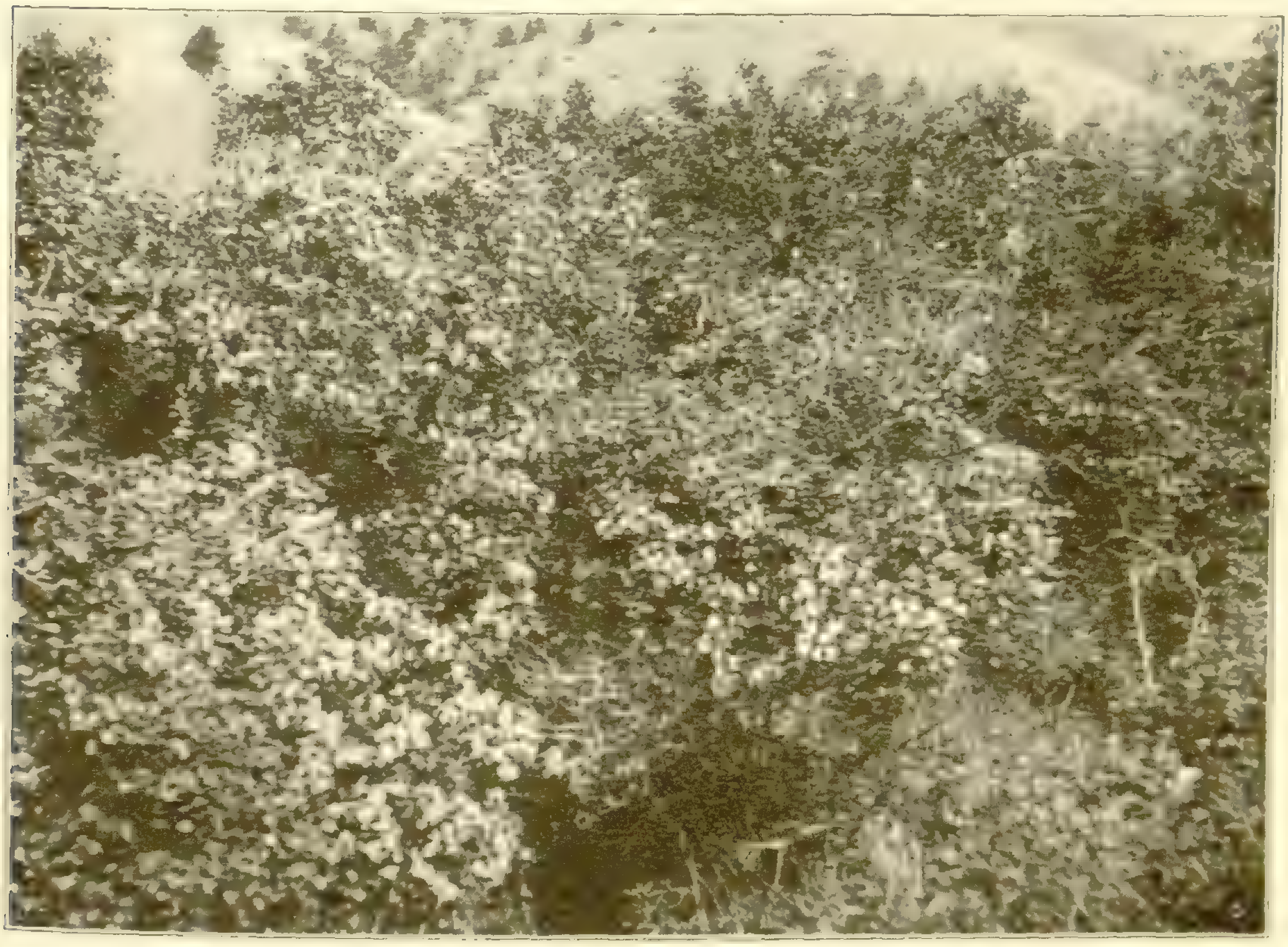

Fig. 6.—A hawthorn society.

cañon is causing the invasion of this formation by various weeds the commonest of which is *Trifolium repens*.

Common species of the middle layer are *Geranium Richardsoni*, *Rudbeckia ampla*, *Aconitum columbianum*, *Aquilegia coerulea*, *Viola canadensis*, *Heracleum lanatum*, and *Vagnera stellata*. Occasionally a *Mertensia ciliata* from the brookside formation of the Hudsonian zone wanders down the cañons to 2250^{m}.

In the upper limits of the formation the cottonwoods are mainly absent, the control here being shared by *Salix Nuttallii* and *Alnus tenuifolia*, with an occasional invasion of *Pseudotsuga mucronata*, *Picea Engelmanni*, *Picea Parryana*, and *Populus tremuloides*. In these places the ground is usually very wet and there are present in the middle layers, in addition to the forms already enumerated, *Senecio triangularis*, *Trollius albiflorus*, *Thalictrum occidentale*, *Oxypolis Fendleri*, *Panicularia nervata*, *Carex variabilis*, *Montia Chamissonis*, *Carex canescens*, *Agrostis hiemalis*, and *Geum oregonense*. The middle layer here is usually open, but occasionally the grasses or Carices form closed societies.

The formation is in a static condition. Within the cañons at least there is no apparent migration of the cottonwoods taking place, though an occasional *Salix Nuttallii* has invaded the mountain slopes to a point outside the proper limits of the formation.

The observations made in a thicket of *Corylus rostrata* and those in a hawthorn society, and recorded under the Populus occidentalis formation, apply equally well to this formation, since these formations overlap at this point, as I have already mentioned. In addition ot these observations, I have three observations taken during the summer of 1907. These observations were made at three stations which I shall call A, B, and C respectively. Stations A and B were in Boulder Cañon about 20^{km} west of Boulder at an altitude of about 2250^{m}, while station C was at the mouth of Boulder Cañon. Station A was 6^{m}, B 6^{dm}, and C 1.2^{m} from the edge of the stream.

My observations follow:

Temperatures

		-75^{dm}	-15^{cm}	0	9^{dm}
Station A.	(June 26, 5 P.M.)	11°	13°	14°	
Station C.	(July 30, 5 P.M.)		16°.5	19°.2	21°.2

		Water content	
		15^{cm}	$17–75^{cm}$
Station A.*	(June 26)	43.7 per cent.	14.6 per cent.
Station B.*	(June 26)	30.0 per cent.	....
Station C.†	(July 30)	21.2 per cent.	....

* Observations made following a period of showery weather.
† Rain two days previous.

(3) THE PINUS–SCOPULORUM FORMATION (*fig. 2*)

This formation covers the dry slopes of the mountains from their base at an altitude of 1650^{m} to about 2400^{m}. It is exceedingly open, the pines seldom exercising any decided control on the surrounding vegetation, except when associated with the Douglas firs. While the Pseudotsuga characteristic of the Pseudotsuga-Picea formation extensively overlaps the Pinus scopulorum formation, I have thought best to consider the two as distinct, because the characteristic habitat of each is distinctly different. Pseudotsuga, in the lower part of its range, is restricted to the north slopes and the cañon bottoms, while *Pinus scopulorum* occurs indifferently over north and south slopes alike, and is absent from the cool, moist cañon bottoms (see below). *Pinus scopulorum* is frequently associated in more or less dense clumps with Pseudotsuga, and where such is the case, or where the pines themselves grow densely, there is present no under layer whatever, with the exception of a few mosses and lichens. As soon as the formation becomes thinned out a little, shrubs and grasses from neighboring areas wander in. *Sabina scopulorum* is found in scattered association with the pines throughout the formation.

According to old residents of the county, the pines were formerly much more numerous than at present, having been largely cut for timber, this species having been formerly the principal timber tree of the mountains. At present comparatively little is being cut. The formation is in a dynamic condition. Large numbers of pine saplings are springing up throughout its extent, and on the mesas, which extend peninsula-like from the mountains on to the plains, are numerous strips of open pine forest, gradually invading the grass land of the plains.[8] An exposed sandstone cliff 11^{km} from the base of the mountains at Boulder bears in a crevice a young specimen of yellow pine.[9] Occasionally *Celtis reticulata*, a representative of the eastern forests, is found invading this formation.

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[8] RAMALEY (*op. cit.*, p. 31) explains the presence of trees on the west end of the mesas and their absence on the east end by a difference in moisture between the two. Since the pines grow on exposed south slopes of the mountains, however, where the water content is very low, this explanation does not appear to me fully satisfactory.

The absence of a secondary layer where the pines and Douglas firs grow densely is not to be explained alone on the ground of a scarcity of light or of moisture, but rather by the combined absence of these factors. The shade is seldom dense enough to exclude shade-loving plants, were sufficient moisture present to satisfy the needs of such forms.

The physical factors of this formation were taken at an altitude of about 2100^{m} on a north slope in a small grove of pines and Douglas firs. The results are given below:

Temperatures

(Observations July 29, 12:15 P. M.; August 14, 5:15 P. M.; September 13, 3:40 P. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+9^{dm}$
Minima......	16°.2*	19°*	18°.75	21°.75	22°
Maxima......	17.25*	20°*	26°	27°	26°.75

* Two observations.

Relative humidity

(Observations July 29, 12:15 P. M.; August 14, 5:15 P. M.; September 13, 3.40 P. M.)

	7.5^{cm}	9^{dm}
Minima.......	21 per cent.	23 per cent.
Maxima	65 per cent.	35 per cent.

Water content

Observations	11.25^{cm}	$22.5-11.25^{cm}$
July 29........	3.7 per cent.	4.4 per cent.
August 14......	3.6 per cent.	2.6 per cent.
September 3....	1.6 per cent.	2.1 per cent.

Light values

September 13.............	3:40 P. M. = 4 : 60 (in medium shade)
	= 4 : 360 (in direct shade of tree trunk)

(4) THE PINUS MURRAYANA FORMATION (*figs. 7, 8*)

This formation replaces the Pinus scopulorum formation at about 2400^{m} altitude and stands between it on the one hand and the Apinus flexilis formation on the other, though it is overlapped by each of these, and indeed the two latter overlap each other at about this altitude. The question may be raised whether the *Pinus Murrayana* forests deserve recognition as an independent formation, or should be classed as a part of one or both of the two just named. Since, however, they occupy a definite zone, between 2400 and 3000^m, only occasionally straying up to 3300^m, which zone is not coincident with that of either of the two others, I have decided so to consider them.

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[9] In this connection see also SHANTZ, "A study of the vegetation of the mesa region east of Pike's Peak: the Bouteloua formation." BOT. GAZETTE 17:185, 186.

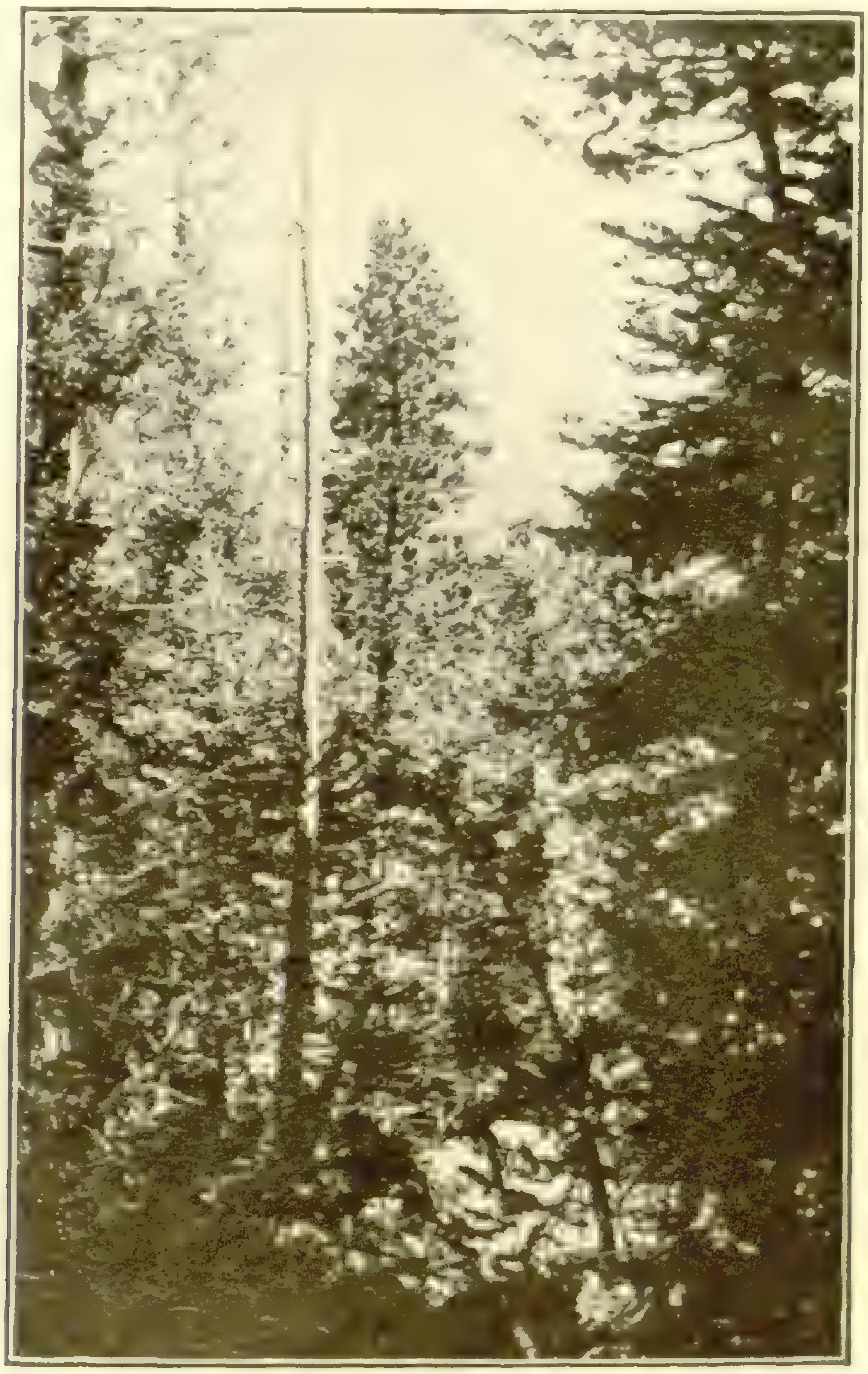

FIG. 7.—*Pinus Murrayana* and Pseudotsuga timber near Nederland, Colorado; approximate altitude 2550^m.

This formation occupies the dry mountain sides and is absent from the cañon bottoms. In the former situations it frequently mingles with the Pseudotsuga-Picea and Picea-Abies formations. Its habitat, however, is distinct from that of either of these. While this formation is much broken, alternating with the Carex-grass-shrub formation of the moraines and with the numerous societies of *Populus tremuloides*, it is less open than either of the other pine formations of the mountains. In some places the trees are separated by an average interval of but a few decimeters, which is usually the case in the younger groves. In the older forests there is ordinarily a greater interval between the trees. The normal abundance of the species in a forest formation in a region which has been burnt and timbered as extensively as have the mountains of Boulder County is obviously difficult to determine satisfactorily. But in comparison of apparently

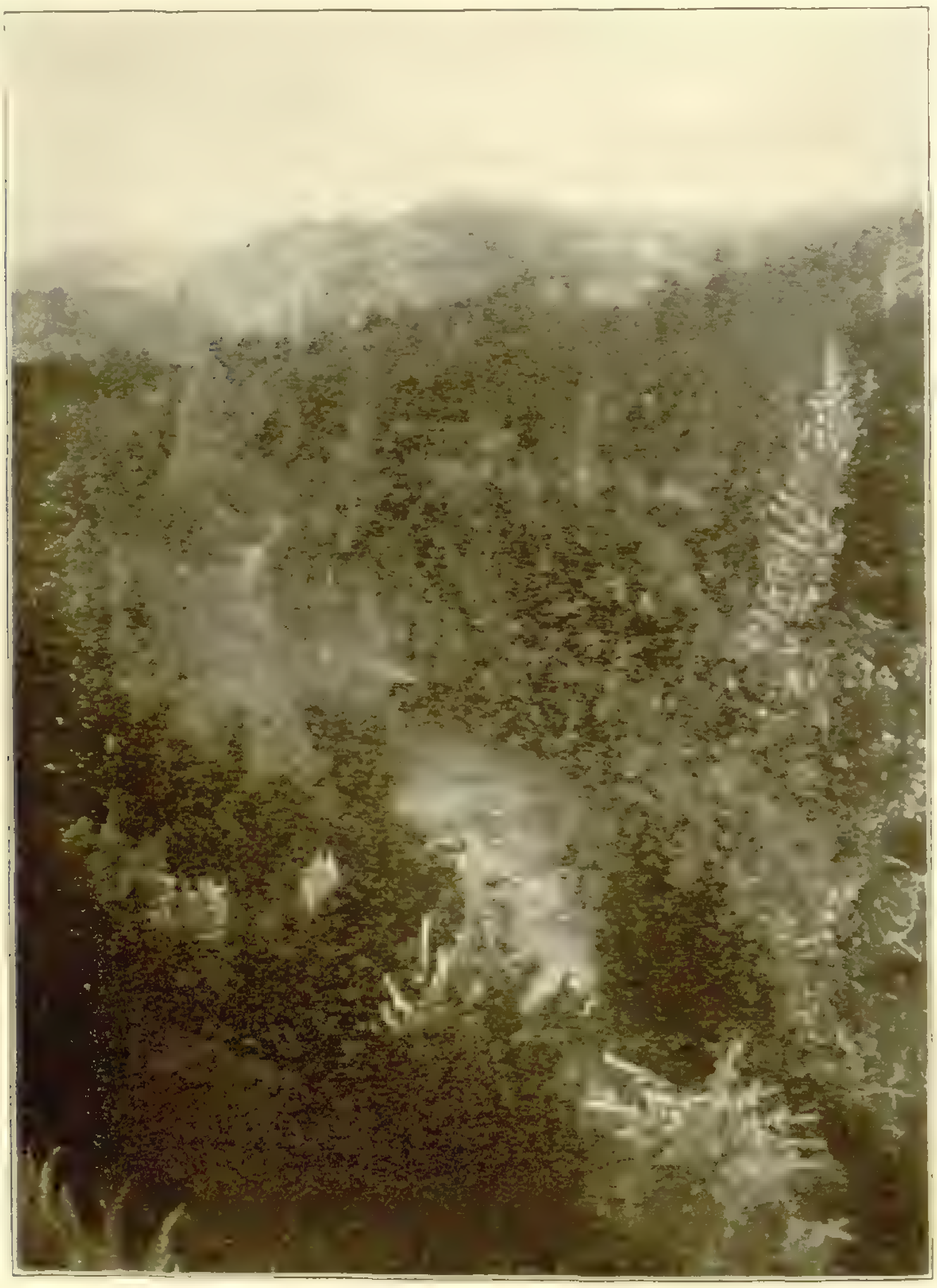

FIG. 8.—Boulder Creek between Nederland and Eldora, approximate altitude 2490^{m}; in the cañon bottom *Alnus tenuifolia* and *Salix Nuttallii* dominate; the cañon sides are clothed with a mixture of the Apinus flexilis, Pinus Murrayana, Pseudotsuga-Picea, Picea-Abies, and Pinus scopulorum formation.

virgin tracts of *Apinus flexilis* and *Pinus Murrayana*, I find that the latter grows more densely than the former. I know of no virgin tracts of *Pinus scopulorum*.[10]

In the denser parts of the formation the under layer is very scanty, and consists mainly of *Pyrola secunda*, *Arctostaphylos uva-ursi*, and *Chimaphila umbellata*, with a few mosses and lichens. Where the formation is more open frequent invaders from the neighboring Carex-grass-shrub formation straggle in. *Razoumofskya americana* is a common parasite of *Pinus Murrayana*. Relative to the damage wrought by this and the preceding species of mistletoe see JACK (*op. cit.*, p. 45).

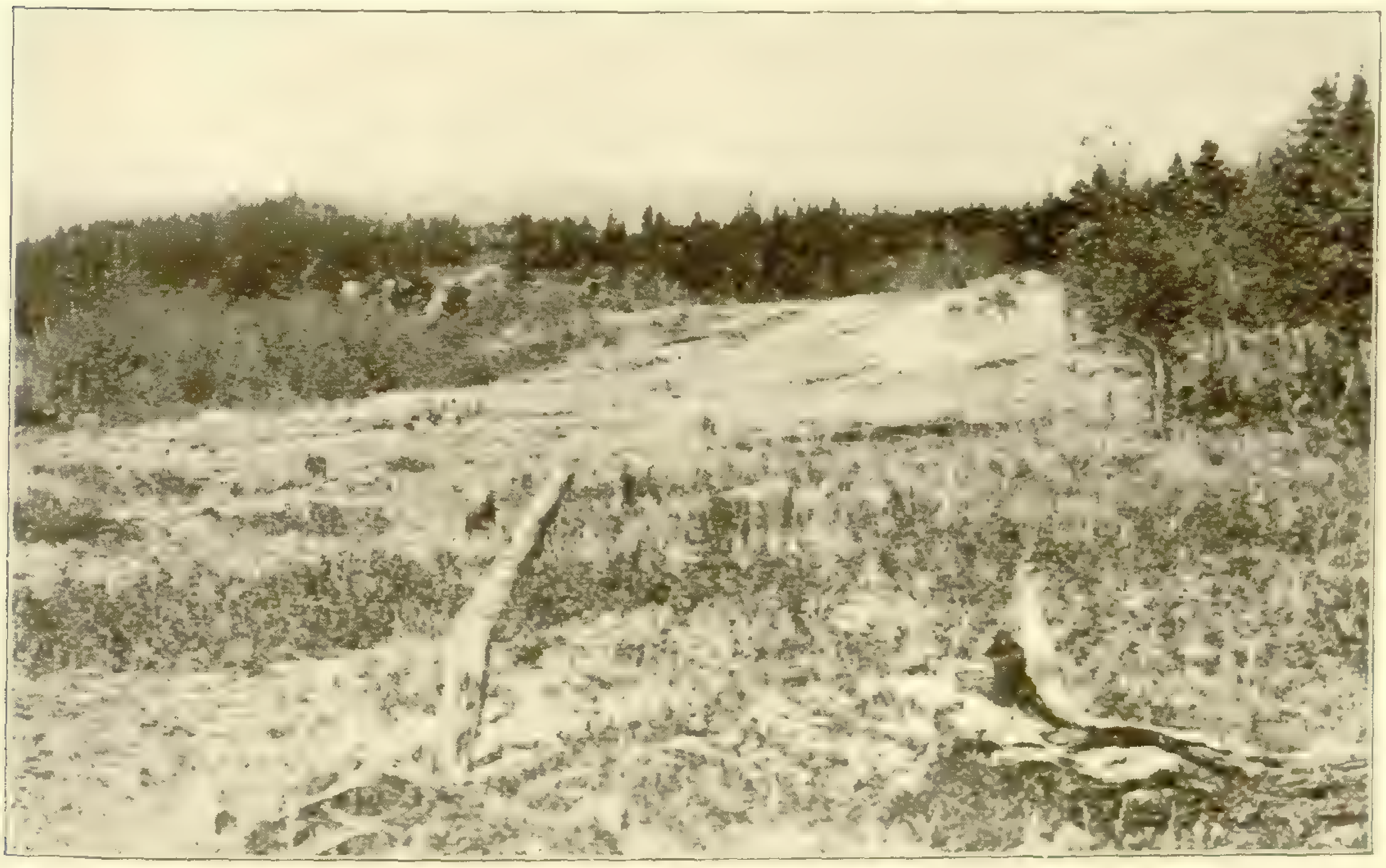

FIG. 9.—*Pinus Murrayana* and *Populus tremuloides* timber, two miles west of Sunset, Colorado; approximate altitude 2700^{m}.

The discussion of the deforestation and reforestation of the areas included in this and the succeeding formations I shall reserve for consideration under "Succession."

Observations of the physical character of the habitat of this formation were taken at two stations. One of these was in a mixed forest of *Pinus Murrayana* and *Pseudotsuga mucronata* at an approximate altitude of 2550^{m}, with a northwest exposure. At this station three sets of observations were taken on July 13, 25, and August 29. The other station, at which but one set of observations was made on August 29, was in a grove of young pines on a northwest exposure at an approximate altitude of 2520^{m}. The first of these I shall call Station A, the second Station B.

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[10] In this connection see also JACK, Pike's Peak, Plum Creek, and South Platte Reserves, U. S. Geol. Survey, 20th Ann. Rep., pt. 5, p. 50.

Temperatures

Station A (Observations July 13, 10:50 A. M.; 25, 3:20 P. M.; August 29, 6:45 A. M.)
Station B (Observation August 29, 1:40 P. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+9^{dm}$
Minima......	9°6	11°	12°5	14°5	15°*
Maxima......	13°	14°5	26°	23°25	20°25

* Two observations.

Relative humidity

Station A (Observations July 25, 3:20 P. M.; August 29, 6:45 P. M.)
Station B (Observation August 29, 1:40 P. M.)

	7.5^{cm}	9^{dm}
Minima.......	43 per cent.	45 per cent.
Maxima.......	67 per cent.	64 per cent.

Water content

	Observations	11.25^{cm}	$22.5-11.25^{cm}$
Station A..........	July 25	9.8 per cent.	6.9 per cent.
	August 29	6.7 per cent.	9.5 per cent.
Station B..........	August 29	5.3 per cent.	4.2 per cent.

(5) THE APINUS FLEXILIS FORMATION

This formation occurs over the dry mountain slopes from 2550^{m} up to timber-line. In the lower part of its range it is represented by only a few scattering individuals, but above 3000^{m} it is the dominant pine formation. Here it extensively overlaps the Picea-Abies formation, but I have thought best not to classify it with the latter as Apinus-Picea-Abies formation, because it occupies as a rule higher, drier ground than the firs and spruces, which are found in the cañon bottoms as well as on the higher slopes.

Even in the virgin forest, the trees are separated by comparatively wide intervals, but their spreading tops meeting overhead produce a sufficiently dense shade to exclude all but a few straggling invaders from the open slopes, with the exception of the mosses and lichens and *Vaccinium microphyllum*, which form the characteristic layer of the forest floor. This last species forms a loose straggling layer in both this and the spruce-fir formation of the high mountains, attaining a height of only a few inches. Biologically, the under layer of this formation is open, but the physical conditions of its habitat are such as to exclude most plants.

Save where artificial conditions such as fire or lumbering have intervened, the continuity of this formation is comparatively unbroken, except in its lower limits, where it is represented only by a few straggling individuals.

Observations of the physical character of the habitat of this formation were made at two stations which I designate as A and B. Station A was on a gentle slope with a southwest exposure, at an approximate altitude of 2940^{m}. Station B was on a comparatively level area at an altitude of approximately 3150^{m}. A series of three observations at these stations gave the following results:

Temperatures

Station A (Observations July 5, 1:45 P. M.; 27, 11:15 A. M.; September 5, 12 M.)
Station B (Observation July 19, 6:30 A. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+0.9^{m}$
Minima......	5°.8*	6°.2	6°	11°‡	11°‡
Maxima......	8°†	8°	13°.4	14.5‡	13°.75‡

* Depth of 17.5^{cm}. † Depth of 20^{cm}. ‡ Three observations.

Relative humidity

Station A (Observations July 5, 11:45 P. M.; 27, 11:15 A. M.; September 5, 12 M.)
Station B (Observation July 19, 6:30 A. M.)

	7.5^{cm}	9^{dm}
Minima...........	34 per cent.	27 per cent.
Maxima	63 per cent.	59 per cent.

Water content

	Observations	11.25^{cm}	$22.5-11.25^{cm}$
Station A..........	July 5	17.3 per cent.	
	July 27	18.5 per cent.	8.7 per cent.
	September 5	21.4 per cent.	5.5 per cent.
Station B..........	July 19	16.1 per cent.	11.7 per cent.

The light value of the Apinus flexilis formation was taken at a point where this formation overlapped the Picea Engelmanni–Abies lasiocarpa formation, on September 8 at 11:30 A. M. The observation was made in the general shade of the forest, not in the direct shade of a tree trunk. The value was 5:180.

(6) THE PSEUDOTSUGA MUCRONATA–PICEA ENGELMANNI FORMATION

(*figs. 7, 8*)

This is the dominant formation of the cañons from 1800 to 2700^{m}. It mingles with the Pinus scopulorum and P. Murrayana formations on the ridges and with the Populus angustifolia formation in the cañon bottoms. *Pseudotsuga mucronata* is more common than the other characteristic of the formation and is far more extensive in its habitat than the latter. Besides *Picea Engelmanni*, *P. Parryana* occurs in the formation, forming a straggling society along the bottom of the cañons from 2100^m to 2700^m. Both of these species are confined to the cool, moist cañon bottoms and the draws running into them. The Pseudotsugas, on the contrary, extend up on to the dry ridges to associate with the pines growing there. They come down the cañons to 1710^m, while the lowest limit of Picea is about 1950^m.

I have already mentioned the fact that Pseudotsuga, in the lower part of its range, is restricted to the north slopes.[11] A comparison of the physical conditions of the opposite slopes of Left Hand Cañon at an approximate altitude of 2100^m was made by me on September 20, 1905. Two stations were selected, one on the south side (north slope) of the cañon and the other on the north side (south slope). The former slope was well covered with aspens, the station being chosen in a little glade among them. The latter slope was sparsely forested with aspens and pines (*P. scopulorum*). Each station was about 9^m above the stream. The former I have designated as A and the latter as B. The following are my results, the observations being made September 20, 1905:

Temperatures

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+0.9^m$
Station A, 2:15 P. M.	7°5	9°5	10°5	20°25	21°7
Station B, 2:50 P. M.	22°5	19°	43°	28°5	25°5

Relative humidity

	7.5^{cm}	9^{dm}
Station A, 2:15 P. M.	32 per cent.	27 per cent.
Station B, 2:50 P. M.	25 per cent.	26 per cent.

*Water content**

	1^m depth	22.5^{cm} depth †
Station A	4.9 per cent.	11.3 per cent.
Station B	2.7 per cent.	3.3 per cent.

* The preceding evening was showery and rain probably fell at these stations.

† A few centimeters core was taken at each depth.

As the result of lumbering and fires, this formation has been extensively invaded by forms from adjoining open slopes, but typically it is a closed formation admitting only a few shade plants. Where it overlaps the pine formations on the ridges, its secondary layer is the same as already described for them. In the cañon bottoms it is invading the Populus angustifolia–Salix Nuttallii formation, while it in turn is invaded by forms from the open cañon slopes. Where the tree growth is dense, however, it is practically exclusive of all forms except a few mosses and lichens and an occasional *Pyrola secunda* or *Arnica cordifolia*. The formation has been lumbered extensively, the Douglas fir being used to a considerable extent for rough bridge timbering and similar purposes.

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[11] In this connection see also JACK (*op. cit.*, p. 434, *pl. 12*); SHANTZ (*op. cit.*, pp. 34, 40); and RAMALEY (*op. cit.*, pp. 31 et seq.).

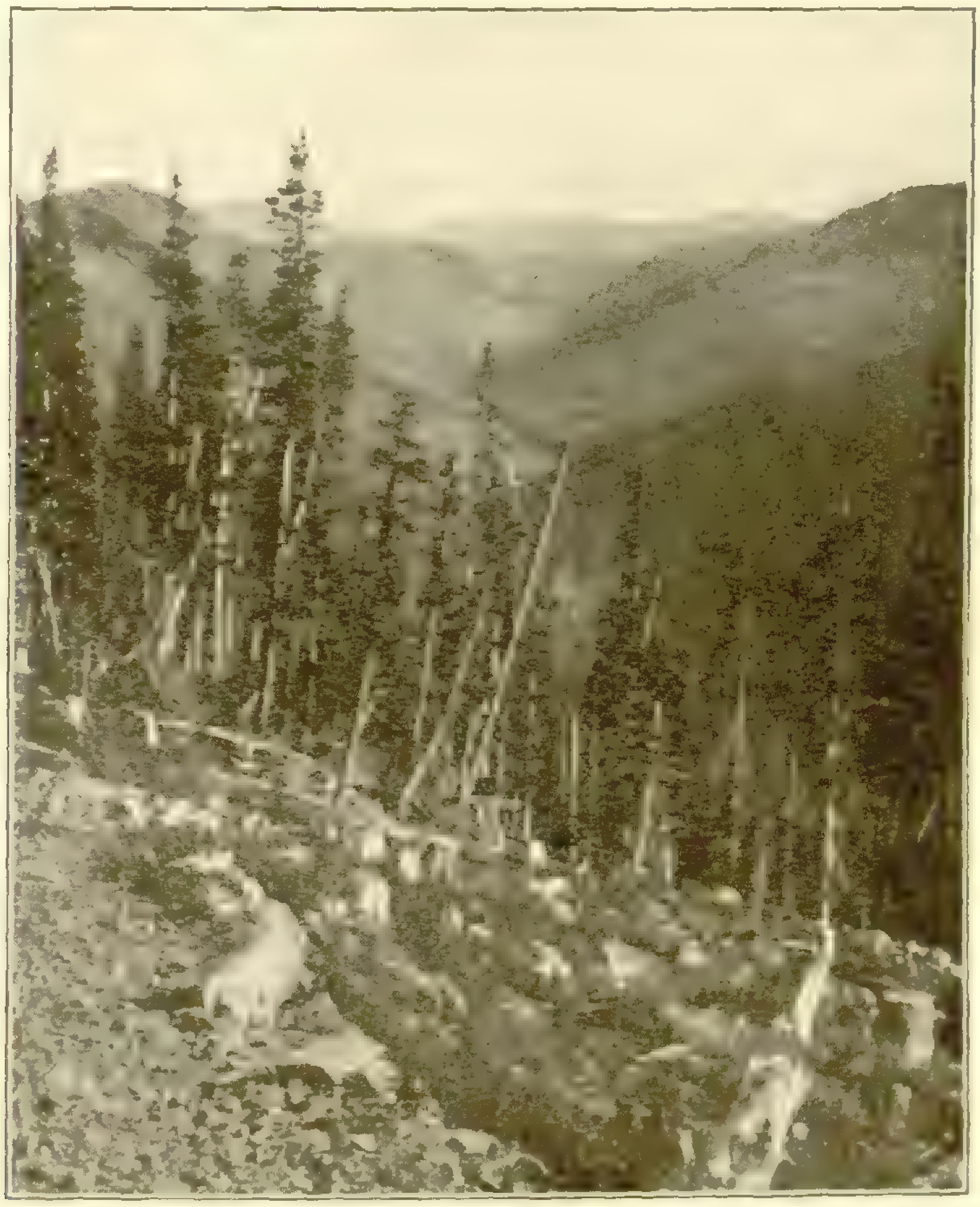

FIG. 10.—The Picea-Abies formation; approximate altitute 3300^m; in the background is seen an extensive burned area.

For the physical characters of the habitat, reference may be made to the results recorded for the Pinus scopulorum formation, and for Station A in the Pinus Murrayana formation, since both of these sets of results are representative of the higher, drier parts of the Pseudotsuga habitat. One other set of observations was made at the bottom of Boulder Cañon at 3:40 P.M. on August 29 at an approximate altitude of 2250^{m}. Here *Picea Engelmanni* is common and the physical factors typical of the cool, moist portions of the habitat of this formation. The results obtained at this latter point are as follows:

Temperatures

-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+9^{dm}$
11°.5	14°	17°	——	18°.7

Water content

11.25^{cm}	$22.5-11.25^{cm}$
135.7 per cent.	5.8 per cent.

(7) THE PICEA ENGELMANNI-ABIES LASIOCARPA FORMATION

(*figs. 4, 10, 11*)

This formation occupies chiefly the cañons and to a lesser extent the ridges of the mountains from 2850^{m} to timber-line, in the latter situation mingling with the Apinus formation. The two characteristic species are of comparatively equal abundance, although the firs are more numerous above 3000^{m} and do not extend much below 2400^{m}; while the spruces are more abundant below 3000^{m} and pass down, as already noted, to 1950^{m}.

Where the forest is virgin it forms a dense growth, excluding practically all forms except *Vaccinium microphyllum* and a few mosses and lichens. Along the wet stream banks through the forest, however, we find the brookside formation of the Hudsonian zone characterized by *Caltha leptosepala*, *Mertensia ciliata*, and *Senecio triangularis*, while occasional invaders from adjoining open slopes occur in the more open parts of the formation. Of these must be noted especially *Erigeron salsuginosus* and *Pedicularis racemosa*. It is doubtful whether the latter form is to be considered as an invader or not. It is more common in open timber than in clearings, but does not occur in the dense forest.

The results obtained from observations in the Apinus flexilis formation are representative of the drier part of the habitat of this formation. In addition to these results are those obtained at two other points within this formation. The first of these, which I shall designate as Station A, was near the head of a wooded cañon, and in its lower part, at an approximate altitude of 3150^{m}. The slope was gentle, the exposure southeast. The second point, which I shall designate as Station B, was in this same cañon at an approximate altitude of 3300^{m}, on a steep south slope.

Temperatures

	Observations	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+0.9^{m}$
Station A* . .	June 20, 7 P. M.	——	——	4°6	8°7	8°7
	June 21, 6 A. M.	——	——	3°2	2°5	2°2
Station B. . . .	September 22, 4 P. M.	7°25	8°25	14°75	——	——

* The observations at this station were made while many snowdrifts still lay in the forest.

Relative humidity

	Observations	$+7.5^{cm}$	$+0.9^{m}$
Station A.	June 20, 7 P. M.	40 per cent.	40 per cent.
	June 21, 6 A. M.	100 per cent.	96 per cent.

Water content

	Observations	11.25^{cm}	$22.5-11.25^{cm}$
Station A.	June 20, 7 P. M.	227 per cent.	—— per cent.
Station B.	September 22, 4 P. M.	20.9 per cent.	20.9 per cent.

Light value

For light value, refer to Apinus formation.

(8) THE ASPEN SOCIETY (*fig. 9*)

I have already stated my reasons for not considering the groves of aspens as a distinct formation. They have an individuality as a society, however, among the other forest formations which entitles them to separate consideration at this point.

This society occurs within the limits of the other formations. It usually occurs as a distinct society, but occasionally loses its individuality, mingling intimately with the trees of the other forests. It is distributed throughout the mountains from 1800^{m} to 3150^{m}, being confined in the lower part of its range to the north slopes, but in the higher mountains being distributed indifferently over both north and south slopes. It may occur either as a scattered grove of trees, exercising but little if any control upon the lower layers of the vegetation; or it may form a forest with the trees growing within a few feet of each other, in which case it does exercise a decided control upon the lower layers.

The physical conditions in such a forest are intermediate between those in the dense spruce and fir timber of the cañon bottoms and the exposed mountain slopes. The height of the trees and density of the foliage is not such as to produce more than a moderate amount of shade, so that the under layer is not composed exclusively of dense shade-loving species, while the amount of moisture retained by the soil is sufficient to support an abundant growth of plants. The under layer is mixed and for the most part open. Some of the more frequent members are *Artemisia tridentata*, *Arctostaphylos uva-ursi*, *Achillea lanulosa*, *Poa triflora*, *Antennaria parvifolia*, *Poa pratensis*, *Aquilegia coerulea*, and *Castilleja acuminata.*

A series of three observations of the physical characters of the habitat of this formation, taken at a point at 2490^{m} altitude approximately, in a little hollow where the general slope was southwest and very gradual, gave the following results,[12] the observations being made July 5, 6:10 P.M.; 25, 4:05 P.M.; August 28, 5:45 P.M.

Temperatures

	-22.5^{cm}	-11.25^{cm}	0^{cm}	7.5^{cm}	9^{dm}
Minima............	14°.5 *	12°	11°.2	11°	11°.5
Maxima............	14°.5 *	16°	19° †	17°.5	18°.25

Relative humidity

	7.5^{cm}	9^{dm}
Minima.......	68 per cent.	55 per cent.
Maxima	89 per cent.	71 per cent.

Water content

Observations	11.25^{cm}	$22.5-11.25^{cm}$
July 5........	17.3 per cent.	——
July 25.......	21.1 per cent.	7.9 per cent.
Aug. 28......	20.9 per cent.	9.1 per cent.

Light value

August 27, 10 A.M. .... =5 : 90

* One observation only, August 28.

† Four observations, this recorded on July 14.

CLEMENTS,[13] recognizes the following forest formations in the Pike's Peak region of Colorado: Pinus edulis–Juniperus (monosperma); Pinus ponderosa–flexilis; Populus tremuloides; Picea Engelmanni and Parryana–Pseudotsuga (mucronata); Picea Engelmanni–Pinus (aristata). The first of these is not represented in Boulder County. My reasons for recognizing the Pinus scopulorum,

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[12] See also the results obtained at Station A on September 20.

[13] CLEMENTS, F. E., Formation and succession herbaria. Univ. Nebr. Studies 4:329–355.

Apinus flexilis, and Pseudotsuga formations as distinct, and for degrading the Populus tremuloides formation to the rank of a society, have been given in detail in the discussion of these formations. *Pinus aristata* is a southern form not occurring in this region so far as I know.

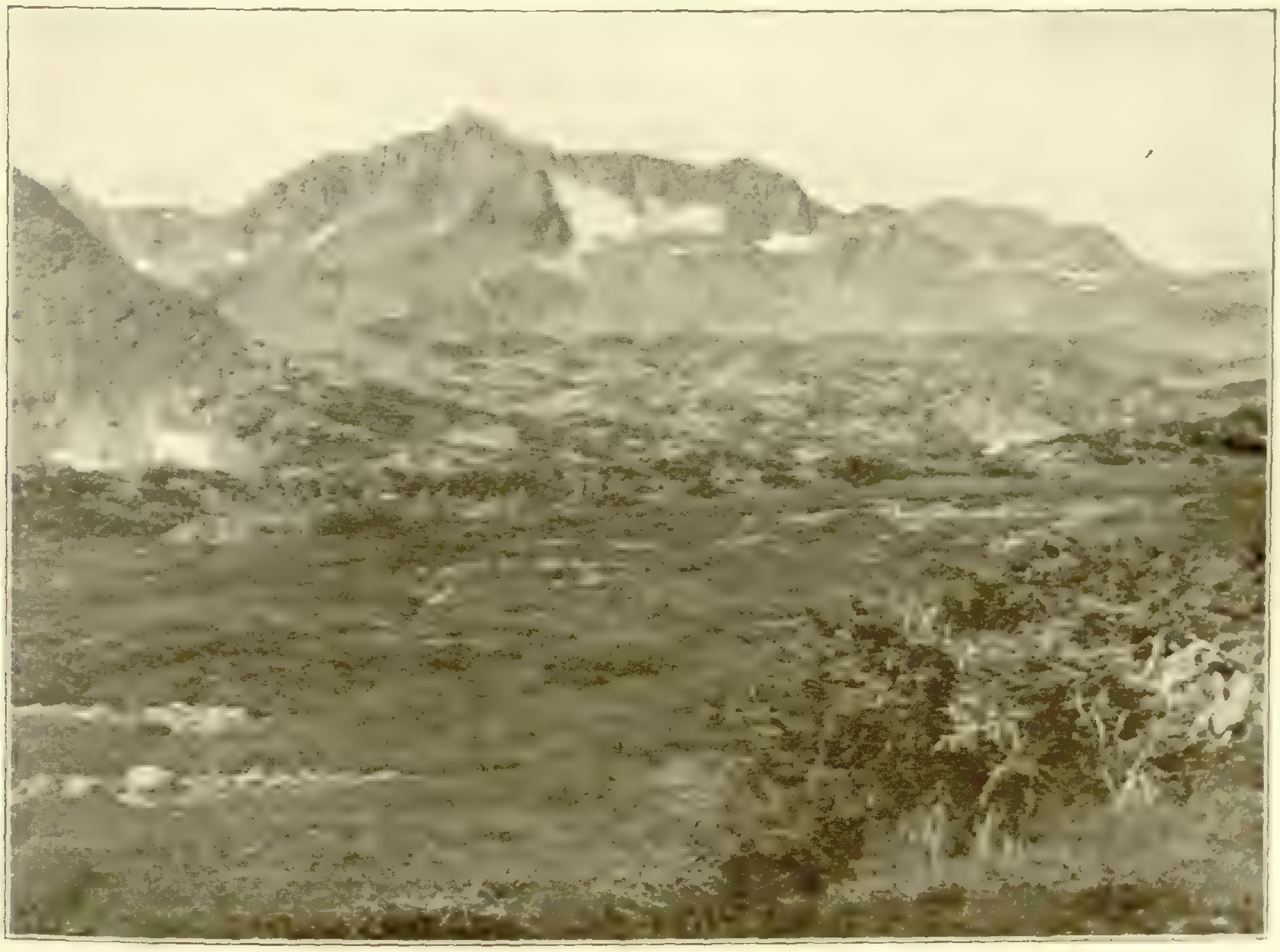


FIG. 11.—Timber-line on Mt. Arapahoe, south slope; approximate altitude 3450^{m}; to the right is a small clump of spruce and fir.

Invasion and succession

The soil of the mountain sides is the result of disintegration of the talus slopes with which they are covered. It is a loose gravel composed of particles of rotten granite, which is very readily eroded and forms an unstable foothold for plants. It is continually working its way downward into the cañons.

I have been unable to determine any sharply defined successional stages within any of the forest formations. The first invaders of a new or denuded soil are determined primarily by proximity, secondarily by mobility. On rough talus slopes, where there has been as yet but little disintegration, the principal forms present are the lichens, but even here occasional shrubs and grasses may be found growing in crevices where a little soil has collected. On loose gravel slopes denuded by erosion, herbs, shrubs, and even trees from neighboring formations, may pass in indiscriminately. Along railroad cuts and embankments and in new soils generally, which are close to highways or other paths of ruderal migration, those forms are among the first invaders, but they are not exclusively the first to enter. Associated with them are forms from the surrounding formations, and these may be either herbs or shrubs, while in some instances trees are the first invaders of a new soil. As an instance of the latter we have the invasion of sand flats on Boulder Creek by *Populus occidentalis*.

All of the forest formations of the higher mountains have been extensively denuded by fire (*figs. 3, 10*). The Pinus scopulorum formation has not recently been burned extensively, due doubtless to the fact that the pines form such a scattered growth that it is difficult for fires to spread to any extent among them. While the aspens play a large part in the reforestation of these burned areas, owing to the mobility of their seeds and the readiness with which they reproduce from roots left uninjured in the burned area, their share in reforestation is not exclusive. Thus any other of the forest trees may reforest a denuded area without the intervention of any aspen stage in the succession, while pines and aspens may reforest a denuded area simultaneously.

In the numerous meadows of glacial origin in the higher mountains, there is proceeding a gradual invasion of the meadows by the Picea-Abies forest adjoining them, the latter representing the final stage in a succession initiated by mosses, sedges, and grasses; these in turn to be replaced by beeches and willows, and these latter finally to make way for the forest. These stages, however, are not sharply defined. The forest may succeed the sedges and grasses directly, without the intervention of willows and beeches, or the latter may succeed the grasses and sedges simultaneously with the forest.

The life-zones of the mountains in Boulder County may be outlined as follows, based upon the forests of the region: *Alpine zone*, characterized by absence of trees, above 3300 to 3450^{m}; *Hudsonian zone*, characterized by *Apinus flexilis* and *Abies lasiocarpa*, 2850 to 3450^{m};

Canadian zone, characterized by *Pinus Murrayana*, 2400 to 2850^{m}; *Transition zone*, characterized by *Pinus scopulorum*, 1650 to 2400^{m}.

While physical factors are so closely interrelated that it is very difficult to separate them in determining what factors exercise the greatest influence in limiting the formations, we may at least limit these factors to two in answering the question "Why are zones present in mountain forests?" The factors of light and humidity may be rejected at once, since their variation at different altitudes is practically negligible. The obvious answer is that mountain zonation is due entirely to temperature. We have already seen that the difference in temperature between timber-line and the base of the mountain is very marked and the same is true, even to a greater extent, of the length of the growing-season. That water content may play as great if not a greater rôle than temperature, however, is at least possible. I have already noted the fact that the rainfall in the high mountains is about 25^{cm} more annually than on the lower slopes.

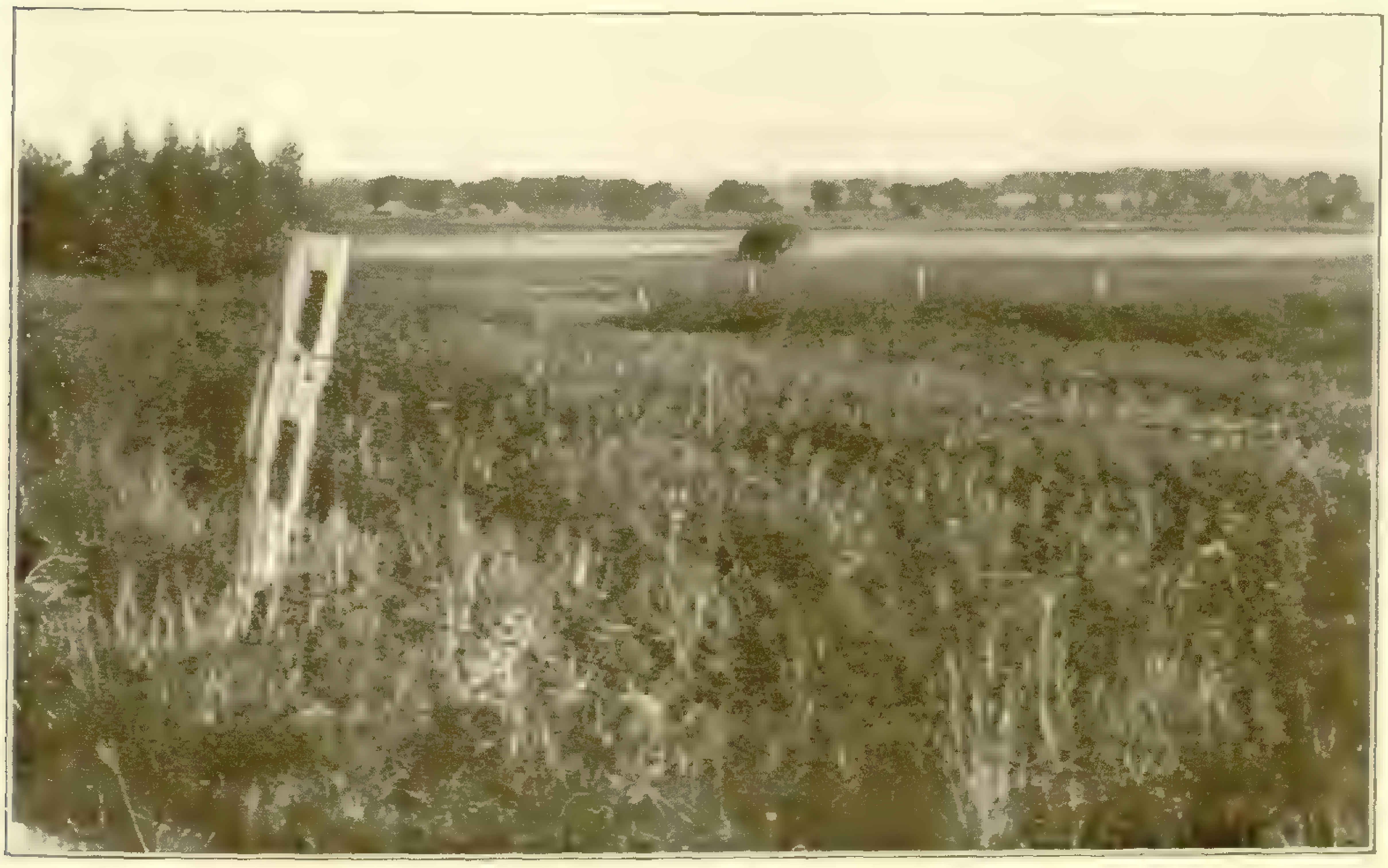


FIG. 12.—The Populus occidentalis formation in the valley of Boulder Creek, six miles east of Boulder; approximate altitude 1590^{m}.

The part played, moreover, by the development of the formations and their relation to the glacial history of the country may be very considerable. At present I have not sufficient data to enable me to discuss this question fully.

In closing this paper, I wish to express my appreciation of the kindly interest taken in my work, and assistance given me by Drs. C. E. Bessey and F. E. Clements, of the University of Nebraska, and by Dr. Francis Ramaley, of the University of Colorado. For identification of my collection I am indebted to the New York Botanical Garden, Professor Aven Nelson, Laramie, Wyoming, and Mr. A. S. Hitchcock, of the United States Department of Agriculture.

University of North Dakota

FERTILIZATION IN CYPRIPEDIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 103

LULA PACE

(WITH PLATES XXIV–XXVII AND ONE FIGURE)

The orchids have attracted much attention on account of their striking habits and especially because of their remarkable adaptations to insect pollination, but the record of morphological investigation is a very scanty one. Morphologists have doubtless regarded them as highly specialized forms, whose interest probably lies within themselves rather than in any connection with the larger problems at present attracting attention. In the stages of development extending from the archesporium of the ovule to fertilization, STRASBURGER'S account (**43**) of *Orchis pallens*, in 1878, indicated that the familiar angiosperm stages were present in the family. Later, the same investigator (**44**) states that no parietal cell is cut off in *Gymnadenia conopsea;* and GOEBEL (**22**) makes a similar statement for *Orchis pallens*, probably based upon STRASBURGER'S original account of this species; but DUMÉE and MALINVAUD (**19**) report several genera with parietal cells. Recently NAWASCHIN (**35**) and STRASBURGER (**45**) have discussed triple fusion in the orchids and its relation to endosperm development, the former claiming that in tropical forms the nuclei remain in contact but do not fuse, the latter stating that fusion occurs in the forms he had investigated. In connection with the development of the embryo, especially in reference to certain remarkable suspensors of the group, there is a considerable body of literature, but it lies beyond the scope of this paper.

The greater part of the material for the present investigation was collected in the vicinity of Chicago in the summer of 1906, small collections having been made also in 1896 and 1898. The collections of 1906 were made June 17, July 4, 11, 17, and 27. *Cypripedium spectabile* and *C. parviflorum* furnished the greater part of the material, but *C. pubescens* and *C. candidum* were examined also in a few stages. The youngest material collected was from flowers just opening, and later stages were collected from time to time until the seeds were almost mature.

MEGASPORE

As is well known, the ovary of orchids contains a great number of small ovules arranged in three double rows. The ovules are very slow in developing, but the archesporial cell is differentiated in the bud. No parietal cell is cut off, the archesporium functioning as the spore mother cell. The young ovule lengthens rapidly and a row of several cells is formed below the archesporium; these cells were often seen in mitosis, but the archesporium was never found dividing until the mother-cell stage. In flowers just opening the spirem of the mother cell is formed, and the synapsis stage is usually reached by the time the flower is in full bloom (*fig. 1*). While the division of the mother cell appears to be of rather long duration in most plants, it seems to be unusually prolonged in orchids as compared with other herbaceous plants. Certain cultivated orchids examined suggest the probability of no further development of the ovule unless pollination takes place. The cells of the ovule are all relatively large, with large nuclei, but the mother cell is quite striking because of its size. At this stage the whole ovule, which is always very small, is growing rapidly, the region of the integuments being especially active. The division of the mother cell takes place in the usual way (*figs. 1, 15, 16*).

Certain details of this division are particularly well shown in my material. After the integuments are started, the spirem begins to thicken, the chromomeres are very distinct, and the thread is quite long, so that it is hardly possible to do more than suggest its appearance in a drawing (*fig. 2*). A nucleus like that in *fig. 3*, in which only a few threads are drawn, shows them beginning to be paired; a little later stage is shown in *fig. 4*, where the threads lie closer together and pairing is more evident, the whole spirem being in this condition. In this stage the chromomeres were not so distinct, but it was evident that the threads were not entirely homogeneous. When the threads have approached each other until the chromomeres almost touch, or even seem to be in contact, the synaptic knot begins to form (*fig. 5*), usually around or close to the nucleolus, which often shows vacuoles at this time. As the threads are crowded more and more into the knot, often several of them seem to be attached to the nuclear membrane (*fig. 6*); this was seen several times, so that it is probably the usual condition. The synaptic knot is at one side of the nucleus and gradually becomes a compact mass (*fig. 7*). Even when it is most compact, the constituent threads are apparently distinct, as is suggested in the figure by the rough edges of the knot and by the very evident lines across it. Hundreds of nuclei in this stage were examined and this seems to be the usual condition.

Upon coming out of synapsis, the threads are no longer in distinct pairs, but in many instances the double nature could be detected for short distances, and occasionally throughout much of the spirem. The threads gradually resume their position near the nuclear membrane (*figs. 8, 9*), and about this time the cytoplasm becomes arranged in lines which radiate from several centers (*figs. 8, 11*), which are evidently the first indications of the multipolar spindle. The chromomeres become less and less distinct, so that with the thick spirem an almost perfect homogeneity seems to exist (*fig. 9*); but even in this stage the double nature of the spirem is often evident, especially when cut ends are examined. There are eleven chromosomes at this reduction division (*figs. 12, 13*), but it was not possible to determine just how the splitting takes place—whether transversely or longitudinally. *Fig. 10* is at the right stage, but whether these pieces are to be regarded as having about completed the longitudinal splitting, or as the one long curved and twisted chromosome which will be cut transversely, could not be determined from my material. *Fig. 15* shows a typical spindle for the division of the mother cell. A cell in the wall of the ovule gave the expected count of twenty-two chromosomes for the sporophyte; these were scattered somewhat in the drawing (*fig. 14*).

When first formed, the daughter cells are alike in form and size (*fig. 16*); but very soon the inner cell shows that it is developing faster than the outer (*fig. 17*), which also begins to show signs of disintegration. This difference becomes more and more pronounced in the metaphase (*fig. 19*) and telophase (*fig. 20*) of the favored cell. Early indications of the spindle suggest the usual bipolar form (*fig. 18*), and longitudinal splitting of the chromosomes is shown in *fig. 19*, so that there is nothing unusual in this division of the daughter cell (or cells) up to the telophase stage. There is no evidence of a wall forming between the two nuclei either in the telophase stage or later; and the two nuclei are thus left free in the cytoplasm. This stage was seen repeatedly, and never was there a wall separating the megaspores formed by the second division. *Figs. 20, 21, 23, 24* represent conditions common in the material studied, which was collected July 11, when the flowers had withered. This is the condition in most flowers when one looks for fertilization stages; but here the megaspores are just forming in many of the ovules, although in an occasional one there was some evidence of fertilization. The figures give a rather complete series of the stages that would be expected to show indications of wall formation; but there is no suggestion of an ephemeral wall even, as might be expected in case of its relatively recent elimination. *Fig. 22* shows two daughter cells in which the nucleus of the micropylar one is developing, but this was the only case of the kind seen.

EMBRYO SAC

Immediately after the division of the inner daughter nucleus, forming two megaspore nuclei with no wall separating them, these two nuclei organize the embryo sac (*fig. 23*), which increases rapidly in size and becomes very vacuolate. The two megaspore nuclei form spirems (*fig. 24*) which thicken, and the usual mitotic division follows (*fig. 25*). The spindles for this division, resulting in a four-nucleate sac, are small and apparently at right angles to one another. No evidence of another division was found, although at least three hundred slides with hundreds of ovules upon each were examined for this particular stage. When the sac is ready for fertilization, four nuclei are present, so that if other nuclei are formed they are very ephemeral. The micropylar daughter cell resulting from the division of the megaspore mother cell may still be distinguished, though it is evidently fast disintegrating (*figs. 23, 24, 25*). The four nuclei of the sac are usually of the same size (*fig. 26*), but in one instance the two micropylar ones were larger than the others (*fig. 27*). Probably *fig.* 28 gives the explanation; in this sac the two megaspore nuclei are not dividing simultaneously, the antipodal one being in late prophase, while the micropylar one has reached the late telophase and the two new nuclei are being organized. Not only has the embryo sac increased enormously in size, but the whole ovule is very active. The integuments have grown very rapidly, having lengthened until they reach far beyond the nucellus.

The usual egg apparatus, with its two synergids and egg, each with very distinct cytoplasm and *Hautschicht*, is organized in the micropylar end of the sac, the other nucleus being left in the center or toward the antipodal end (*figs. 29, 30*).

A few peculiar or "abnormal" forms were found. *Fig. 31* shows what appears to be two mother cells, which is suggested by the unusual development of that region of the ovule compared with that of the integuments and the remainder of the ovule; but the best evidence is in the chromosomes, which in both cells appear to be of the heterotypic form. In another orchid, in several cases, two mother cells (in synapsis) were seen in a single ovule. Usually the spindle in the division of the mother cell is parallel with the axis of the ovule; but *fig. 32* shows one at right angles to the usual position; only two of these spindles were seen, and they were near each other in the same ovary. No arrangement of megaspores seen could be related to this position of the spindle. Several examples of the division of both daughter cells were found (*fig. 33*). It is probable that in this case only one embryo sac is formed, for even in the very early spirem stage the two chalazal megaspores are developing at the expense of the others, or at least more rapidly than the two micropylar ones (*fig. 34*). The width of the ovule in *fig. 35* suggests the possibility of a transverse spindle, but it was evidently transverse in the second division, as suggested by the lines of protoplasm and by the position of the nuclei. These "abnormalities" are all rare in my material, not more than a dozen such cases appearing among thousands of the usual forms.

FERTILIZATION

The immense number of ovules suggested the possibility of parthenogenesis, or of failure to develop an embryo at all. The latter view is favored by the well-known difficulty in germinating orchid seeds, but the material studied gave no indication of either condition. All ovules of the right age had embryos, and in almost all of them evidences of the pollen tube were more or less distinct, traces of it often being detected in the space between the wall of the ovary and the micropyle; and in most cases traces could be seen in the micropyle and continuing into the embryo sac (*figs. 43, 49*).

In the pollen grain the division into tube end generative cells takes place before shedding. In this division a wall forms in all cases examined, but it soon disappears. In one anther over one hundred late anaphases and early telophases were counted in which the wall was formed, and only about a dozen late telophases were without a wall. As these showed no traces of the spindle, the probability is that the wall was formed here as in the others, but had disappeared. The generative nucleus has a mass of cytoplasm about it that differs markedly in its staining reaction from that of the tube nucleus. The gametophyte number of chromosomes (eleven) was easily counted here. *Figs. 36–41* represent a series in this division. *Fig. 39* shows the wall forming in the telophase, while *fig. 40* shows it completed. The latter figure is also interesting in showing a chromosome left out of one of the nuclei at its organization.

The division of the generative nucleus was not seen; but as pollen from the bud to the time of shedding was studied, it must take place after pollination. When the pollen tube is passing from the ovary wall to the micropyle, the division has already taken place (*fig. 45*).

Only one attempt at pollination was made. Two flowers with stems about 25^{cm} long were brought into the laboratory, placed in water, and the whole put under a bell jar with some ventilation to keep them in as nearly normal condition as possible. Each was pollinated from the other. Four days later one of them was fixed, being apparently in good condition; but the other was dead six days after pollination. When the first was sectioned and stained, the ovules were found to have gone to pieces. The pollination was made in the hope of getting some idea of the development of the ovule in relation to the time of pollination. The stigma was sectioned and showed that the pollen grains had practically all developed tubes, many of them being traced into the conductive tissue, in some cases for some distance, and the grains were almost all empty. If the development of the tube was delayed, a condition like that in *fig. 41* was found, in which the tube is just forming and the generative nucleus is beginning to show signs of activity. Soon a complete spirem is formed, and tubes less than the length of the pollen grain have the three nuclei in them; so that the generative nucleus probably divides into the male nuclei as the tube develops.

It will be remembered that the embryo sac ready for fertilization contains only four nuclei—the egg apparatus in the usual position, and the remaining nucleus near the center of the sac or toward the antipodal end (*figs. 29, 30*). As the pollen tube penetrates the sac, one of the synergids may be in front of it and a little lower than the other, as if it were being pushed from its usual position by the inrush of the contents of the tube, or moving for some other reason toward the antipodal end of the sac (*fig. 44*). The egg nucleus may be already in the spirem stage. The pollen tube here shows the tube nucleus in advance, with the two male nuclei elongated and near it. A stage just later than this shows two nuclei below the egg, and from the lines of cytoplasm one seems to be the synergid which has moved to that position (*fig. 42*). The two male nuclei are still somewhat elongated and are in advance of the tube nucleus. *Fig. 43* shows the polar nucleus and the synergid near the antipodal end of the sac, and the two male nuclei still elongated. The primary endosperm nucleus is formed in this case by the fusion of a male cell, the solitary polar nucleus, and the migrating synergid. In this fusion, as well as in the fertilization of the egg, the fusing nuclei often come into contact in the resting condition (*fig. 45*), the figure showing the male nucleus in contact with the egg still curved and elongated. Many views of this stage might be given with slight variation in the position of the nuclei; and while fusion in the resting condition was apparently the more common in my material, it was not at all uncommon to find spirems already well formed and in different stages of development.

The pollen tube was often traced from the ovary wall through the micropyle into the embryo sac. The male nuclei are usually elongated and sometimes in advance of the tube nucleus, but the tube nucleus usually precedes them (*fig. 46*). In no case does the pollen tube pass directly to the micropyle, but bends in various directions. This may be due to the attraction of other ovules, several of which will be almost as near as the one entered. It may be that after leaving the ovary wall the tube simply wanders in this space until it comes within the influence of the ovule it enters.

One sac indicated the possibility that the synergid may fail to unite in the triple fusion. *Fig. 47* is unusually interesting. Some of the nuclei show the tendency to become amoeboid, but the interest is due especially to the condition of the nuclei, all of those that take part in double fertilization having reached the spirem stage not only before fusion, but even before contact. The spirem is well formed in every nucleus, and shortened almost enough to segment into chromosomes. It would seem in this case that if fusion does take place, there could be no possibility of a fusion of the chromatin, which would certainly divide into chromosomes from each spirem as it is now formed. Well-formed spirems in different stages of development are common; in *fig. 48* the male and female nuclei have formed thick spirems which are evidently distinct, and while those of the triple nucleus are just as distinct, they are much younger. In the same figure an unusual development of the synergid, or possibly of the tube nucleus, is shown; but as no further indication of division was ever found, there is probably no significance to be attached to it. *Fig. 49* shows a pollen tube from its entrance into the micropyle to its ending in the sac, the male nuclei being not only elongated but curved. In a few instances there is some distance between the two male nuclei (*fig. 50*), but this seems to be rather uncommon. The very sharp bend in the tube shown in the last figure suggests some special attraction felt just at this point, directing the tube into the micropyle.

ENDOSPERM

The fertilized egg may divide before the primary endosperm nucleus (*figs. 51, 52*) and during this division the latter may be in the spirem stage (*fig. 51*), or resting, or with the spirem just forming; and in one instance the division of the egg was taking place before the second male nucleus had left the pollen tube. The endosperm nucleus, however, may divide first, *fig. 53* showing it in late prophase while the egg and male nucleus are barely in contact and the spirem is just beginning to be formed in each.

With the nuclei of both fusions in the spirem stage the endosperm nucleus may be farther advanced than the egg, one preparation showing its threads very distinct and much thicker than those of the egg. *Fig. 54* shows a two-celled embryo and the primary endosperm nucleus in late prophase. At the three- or four-celled stage of the embryo, the endosperm nucleus shows a spindle forming (*fig. 55*), which is almost complete and is very broad; the chromosomes (approximately thirty-three) are probably in metaphase. On the other hand, the primary endosperm nucleus may reach the anaphase before the fusion of the male and female nuclei, as one of my sections shows, the male nucleus not having left the pollen tube, and both it and the egg nucleus with spirems forming.

The telophase of the endosperm spindle shows a wall (*fig. 56*), but it is probably ephemeral, as none was seen either in two- or four-nucleate endosperm. The endosperm nuclei are relatively large, as would be expected from the large amount of chromatin used in their formation (*figs. 57, 58*), one in *fig. 57* measuring 17 × 23 μ. For this reason they are not likely to be confused with other nuclei of the sac. The two-nucleate stage of the endosperm may be reached at any stage of the embryo between two and twenty or more cells. The figures for the second division of the endosperm were not seen, but the four-nucleate stage was found in a few sacs (*fig. 58*). From the appearance of these nuclei it is altogether probable that another division may take place, for they are apparently beginning the formation of the spirem for the next division, and are large, vigorous-looking nuclei.

While the presence of endosperm nuclei is quite common, it is not difficult to select a series that would indicate the possibility of their failure. An embryo of several cells with the primary endosperm nucleus still in the resting condition is rare (*fig. 59*); but we need not conclude that division may not take place later than this, for with a still older embryo (*fig. 60*) the endosperm nuclei have begun to form spirems, although there is no evidence of fusion further than the contact. In *fig. 61* one of the nuclei, probably the male nucleus, has been delayed in reaching the other two; yet some suggestion of the spirem is evident in all three. *Fig. 62* shows a sac which is almost filled by the embryo, and at the base are three nuclei which are probably the constituents of the triple fusion which has not taken place; it is barely possible that they are endosperm nuclei, but there is no evidence of a fourth nucleus. If these are not endosperm nuclei, it is evident that in this case none will be formed, for all of them show signs of disintegration.

EMBRYO

The embryo is very simple. As stated above, the fertilized egg may divide before the primary endosperm nucleus, which seems to be the more common behavior in my material; or the primary endosperm nucleus may divide first (*figs. 51–55*). An inconspicuous suspensor of one or two cells is formed, but no other differentiation of regions could be made out in the younger stages (*figs. 55, 62*). The number of chromosomes in the segmentation of the egg seemed to be twenty-two (*figs. 51, 52*), and this number was counted several times in various parts of the ovule (*fig. 14*).

DISCUSSION

It is unfortunate that there is no definite name for the two cells resulting from the division of the megaspore mother cell. "Daughter cells" has been used in this paper to designate them. It has been customary to call the cell that develops the embryo sac a megaspore, and this is correct in all cases when the sac is organized from the chalazal cell in the "row of three" or from one of the cells in the "row of four." But if the name is applied to one of the "daughter cells" there is confusion, for in this case the reduction process is not complete.

MEGASPORE.—In angiosperms two types of embryo sac have been recognized: (1) the more common type, in which the mother cell gives rise to four megaspores, one of which develops the sac; (2) the Lilium type, in which the mother cell, "functioning as a megaspore," forms the sac directly. In the former case, the occasional "row of three" does not change the situation, for the functioning megaspore is derived from the mother cell by two successive divisions (COULTER and CHAMBERLAIN **16**).

The production of only two "megaspores" ("daughter cells") by the mother cell has been reported for a few plants that usually form megaspores in the normal way. SCHNIEWIND-THIES (**40**) reports two or four in Galtonia; GUIGNARD (**25**) two in Agraphis, Ornithogalum, and Commelina; MOTTIER (**31**) two in Arisaema (in one instance with no wall between them, which would present the

Lilium condition); CAMPBELL (**7**) two or three in Dieffenbachia; and JUEL (**29**) two in Taraxacum. The very few cases reported show the rarity of this condition among the angiosperms investigated. Four of the five families represented in this enumeration, to which the Orchidaceae are now added, are all monocotyledons; and this fact, taken together with the still greater reduction in the Lilium type, is in harmony with the theory that monocotyledons are a specialized offshoot from dicotyledons, as held by JEFFREY (**28**), QUÉVA (**37**), Miss SARGANT (**38**), and others.

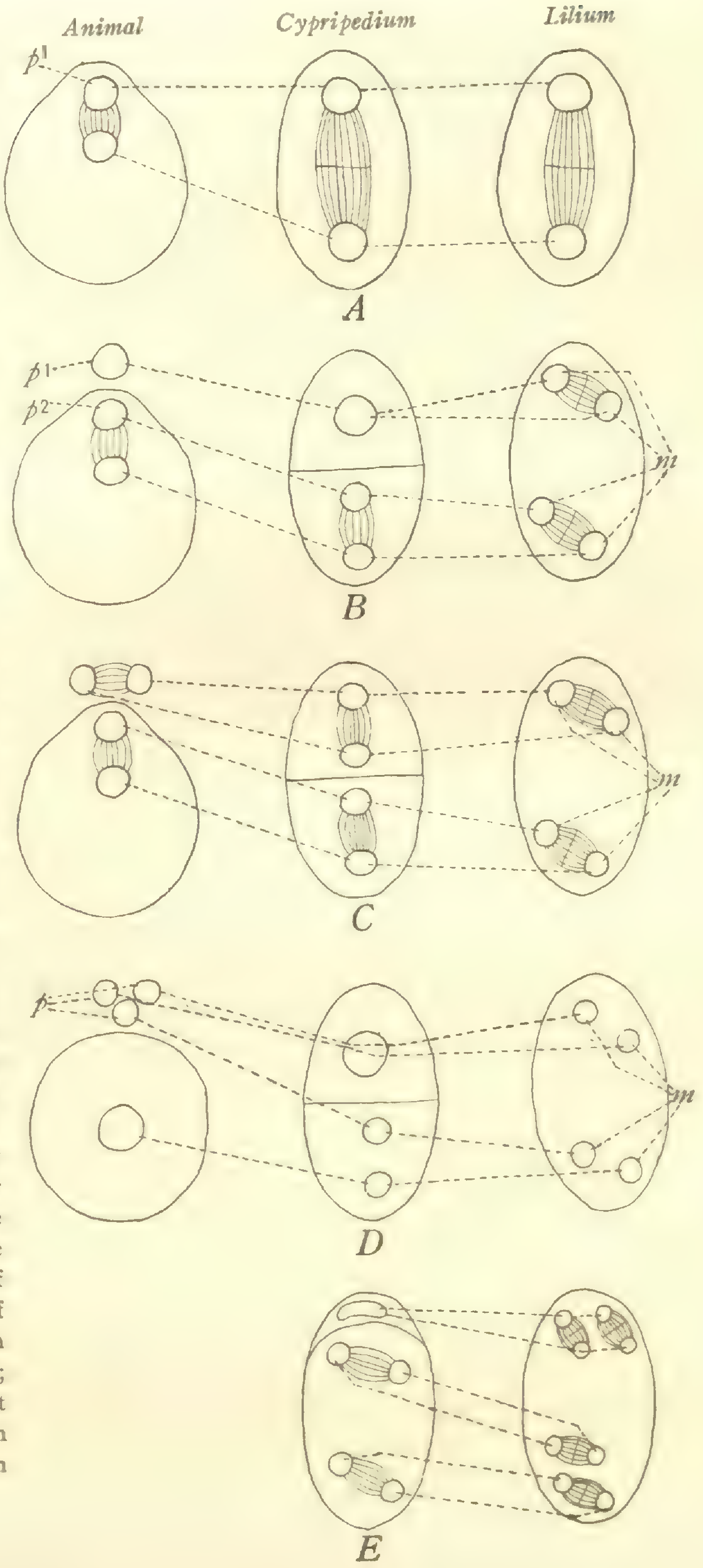
However, SCHNIEWIND-THIES (**40**) has shown that in Lilium the heterotypic and homotypic divisions take place within the embryo sac; that is, there is no permanent wall formed in either of the divisions from mother cell to the four megaspore nuclei. It follows, therefore, that all four megaspore nuclei take part in forming such an embryo sac. In Cypripedium, on the other hand, a wall accompanies the first division of the mother cell, but no wall is formed in connection with the second division. In this case, therefore, two megaspore nuclei enter into the formation of the embryo sac, instead of four as in Lilium, or one as in most angiosperms. It is interesting to note here that if the usual megaspore walls were formed in Lilium and in Cypripedium, each sac would contain two nuclei—the egg and its sister, which is the polar that usually unites with the antipodal polar to form the primary endosperm nucleus.

EMBRYO SAC.—An embryo sac with only four nuclei has not been reported before, but there is just the same number of divisions between the mother cell and the egg in this case as in Lilium. After all, the essential feature in the history of the egg is the distribution of the chromosomes in the reduction divisions. It is possible that the use of more than one megaspore in organizing the sac holds some necessary relation to "double fertilization," for in both Lilium and Cypripedium, if walls appeared in the usual way so that only one megaspore was used in forming the sac, and there were no additional divisions between mother cell and egg, there would be only two nuclei in the sac, and "double fertilization," at least "triple fusion," would be impossible.

It is interesting in this connection to compare this series with that in the animal egg. There the primary oocyte (mother cell) divides and throws off a polar body, and forms the secondary oocyte. The polar body may divide; the secondary oocyte divides, forming another polar body and the mature egg (megaspore) (see BOVERI **6** and WILSON **47**). The two divisions are of the heterotypic and homotypic types found in plants in the formation of megaspores. In Cypripedium, if the last division in the embryo sac were omitted, there would be the same number of divisions in the formation of the egg as in the animal. If the wall were omitted between the daughter nuclei at the division of the mother cell, as in Lilium, and the last division were omitted, the sac would have four nuclei as now; and this would be true of Lilium if the last division did not take place. This situation was discussed by CHAMBERLAIN (**11, 12**) in connection with the usual eight-nucleate sac, and also in relation to the probable four-nucleate sac of Cypripedium.

The situation may be made more clear by means of diagrams. *Fig. A* represents the primary oocyte dividing in the usual way and the mother-cell division in Cypripedium and in Lilium; in all cases this is the heterotypic division. *Fig. B* represents the next division if the first polar body fails to divide, and if the micropylar nucleus fails as in Cypripedium. *Fig. C* represents the same stage as *fig. B*, but the first polar body and the micropylar cell in Cypripedium divide; this is the homotypic division. *Fig. D* represents the division indicated in *fig. C* completed, with the typical arrangement of nuclei in all three forms. This completes the animal series; but in Cypripedium and in Lilium there is another division, which is represented in *fig. E*. It is evident that in these forms there is even greater reduction in the number of divisions than in the male gametophyte if the mother cell be taken as the beginning of the gametophyte generation, as is done by COULTER and CHAMBERLAIN (**17**); for there the male nucleus represents two divisions beyond the microspore, while in Cypripedium and Lilium the egg is removed by only one division from the megaspore nucleus.

WALL IN POLLEN GRAIN.—The ephemeral wall in the pollen grain between the tube and generative nuclei is not difficult to explain according to present homologies. It has been reported in a few plants, as Neottia (GUIGNARD **26**), Sarcodes (OLIVER **36**), Naias and Sparganium (CAMPBELL **8, 9**), Populus and Lilium (CHAMBERLAIN



Successive stages in maturation of animal egg, and in development of megaspores in Cypripedium and in Lilium. *A*, the division of the primary oocyte to form the first polar body (p^1) and the secondary oocyte; and the division of the mother cell in Cypripedium and in Lilium—all heterotypic divisions. *B*, the division of the secondary oocyte to form the second polar body (p^2) and the egg; and the second division in Cypripedium and in Lilium, giving the megaspores (*m*)—the homotypic division in all. *C*, the same stage as the preceding, but the first polar body of the animal and the micropylar nucleus of Cypripedium dividing. *D*, the egg and the three polar bodies (*p*) of the animal, and the megaspores (*m*) of Cypripedium and of Lilium. *E*, not in the animal series; the division that gives the egg in Cypripedium and in Lilium.

13, 14), Sagittaria (SCHAFFNER **39**), Convallaria (WIEGAND **46**), Asclepias (FRYE **21**), and Hamamelis (SHOEMAKER **41**). If the tube cell represents the wall cells of the antheridium, this wall is a relict of the time when there was a complete separation between spermatogenous and wall tissue (COULTER and CHAMBERLAIN **18**). This difference was shown not only by separating walls but by reaction to stains; and the latter difference still remains in the pollen grain after the wall disappears.

DOUBLE FERTILIZATION.—In looking over my material it seems strange that double fertilization was first reported less than a decade ago, when NAWASCHIN (**33, 34**) made his announcement. In my material double fertilization was observed in hundreds of instances; in fact there would be some difficulty in finding fertilization without some suggestion of triple fusion; it was as evident in every respect as the fertilization of the egg. However, it was stated above that in some cases it may fail to take place; and it would not seem unlikely that in some orchids triple fusion always occurs and in others it may be rare or omitted altogether, as indicated by STRASBURGER and NAWASCHIN. NAWASCHIN thought that in the failure of triple fusion he had found the explanation of the lack of endosperm in orchids, but it is evident that the little or no endosperm of this family must be referred to other causes. It may be accurate enough for taxonomic purposes to say "no endosperm" in the orchids, as in a recent manual (**42**), but it is not an exact statement.

DISTINCT PATERNAL AND MATERNAL CHROMOSOMES.—Some important evidence on this much-discussed question was obtained. This condition was first reported in plants by KRUCH (**30**), who worked with the liverwort, *Riella Clausonis;* but at that time (1891) it attracted little attention and seems to have been entirely overlooked by later workers. KRUCH showed the sperm entering the egg and segmenting in the upper part of the cytoplasm, while the chromatin of the egg-nucleus segments near the center, each showing eight chromosomes, and the nuclei were not even in contact. BLACKMAN (**2**), working with *Pinus sylvestris*, figured two groups of chromosomes in the first division of the fertilized egg and says: "there can be little doubt that these bodies are really the chromosomes of the two (male and female) nuclei." In his summary he makes the positive statement that they are the chromosomes of the male and female nuclei. CHAMBERLAIN (**15**) in *Pinus Laricio* finds that "the chromatin appears as two distinct masses in the spirem stage. Perhaps segmentation of the two spirems occurs while they are still separate." MURRILL (**32**), working with *Tsuga canadensis*, says: "The chromatin of each (sperm and egg) nucleus collects in the form of a thick knotted thread near the center of the separating partition, and the two masses remain distinct until the spirem band begins to segment." Miss FERGUSON (**20**), using Pinus, finds "two groups distinct at time of segmentation of spirem and can still be made out during early development of chromosomes; but cannot be when they are being oriented on the nuclear plate." Recently HARPER and BLACKMAN have shown interesting features in some of the fungi that seem to be related to this independence of chromosomes. HARPER (**27**) has shown in Phyllactinia that "the material of each chromosome is in permanent connection with the central body throughout the stages of nuclear fusion and the resting condition, as well as in mitosis." BLACKMAN (**1**) says that rusts which have the aecidial stage have two nuclei in all cells from the aecidiospore to the teleutospore. The two nuclei fuse in the teleutospore and from there to the formation of the aecidiospores the cells are uninucleate. More recently GRÉGOIRE (**23**), working with roots of Allium, claims that the chromosomes do not unite to form a continuous spirem in the telophase, but always remain distinct bodies.

In my material, as shown above, it is quite common to find both the fertilized egg nucleus and the triple-fusion nucleus with distinct spirems in all the nuclei entering into the fusion (*figs. 42, 43, 44, 47, 48, 51, 53*). In one instance the spirems were all well advanced, so that the threads were quite broad, before contact of the nuclei (*fig. 47*). Spirems as far along as these will evidently be cut into chromosomes without fusing at all. If spirems are often formed separately, it would seem probable that when the nuclei fuse in the resting stage two separate spirems may still be present. Anyone who has tried to trace a spirem will at once recognize how difficult it would be to trace two of these long threads in the same nucleus; and as no one expected to find two, only one was seen until two were found distinctly separated. If there may be two spirems in the first division of the sporophyte, why might it not be true of all the mitoses in the sporophyte generation? This would make half of the chromosomes paternal and half maternal in every sporophyte cell. Thus in the mother cell two spirems would be formed as usual, but here they would pair and fuse more or less completely in synapsis. If there are two phenomena in fertilization—stimulus to growth and the mingling of ancestral qualities—only the first would be felt in the sporophyte. The mother cell would give the opportunity for the second during the fusing of the pairs of threads.

The chromosomes of the fusing nuclei are often arranged in groups, and while these may not be definite enough to be positive evidence for distinct chromatin if taken by themselves, they are not only very suggestive but appear as distinct as the position of the nuclei in the spirem stage would lead one to expect (*figs. 51, 54*). In a form in which the paternal and maternal chromosomes differ, proof could be obtained; but even in Cypripedium, in such groups as those shown in *figs. 51–54*, the chromosomes are evidently of separate spirems. This seems very clear when these figures are studied in connection with those showing the spirems (*figs. 42, 43, 44, 47, 48, 51, 53*). The groups are just about as distinct as would be expected, for the nuclei usually overlap slightly in the spirem stage.

SYNAPSIS.—BERGHS (**3, 4, 5**), GREGORY (**24**), CARDIFF (**10**), and others have recently discussed synapsis and the stages leading up to and following this condition. It seems to be clearly established that in the forms studied by these authors there is a gradual pairing of the threads, beginning with the first suggestion of synapsis. The two threads are apparently united into a single thread by the time the nucleus comes out of synapsis. During synapsis itself and in early stages of the recovery from this condition some traces of the double nature of the thread are often seen, and the heterotypic chromosome is formed from this doubled thread. These stages were well shown in my material (*figs. 2–11*). BERGHS sees in this a device for reducing the number of chromosomes, but it may also furnish the opportunity for mixing of parts, or transfer of substance, or influence from the paternal and maternal chromosomes that have remained distinct throughout the sporophyte stage. CARDIFF (**10**) thinks the position of the synaptic knot may be due to gravity. This does not seem to be true in Cypripedium, for the knot was found at all possible positions next the nuclear membrane in serial sections of the same ovary, and even in the same section. This was not only true for cross-sections, but also for longitudinal sections in which, since the ovary stands erect, gravity effects ought to be apparent. BURLINGAME (6a) has reached this same conclusion in his study of Ophioglossum.

SUMMARY

1. In Cypripedium two cells are formed by the mother cell, a wall not appearing in the second division, even in the rare instances in which the nuclei of both daughter cells divide. Two megaspore nuclei are used in forming the embryo sac, the Lilium type using four, and most angiosperms only one. The two megaspore nuclei in the sac of Cypripedium and the four in that of Lilium may be related to double fertilization.

2. Cypripedium has only four nuclei in the completed embryo sac. The Lilium type and Cypripedium have the fewest divisions from mother cell to egg reported among angiosperms. A comparison with the animal egg shows only one more division from the mother cell to the egg in Lilium and in Cypripedium than in the maturation of the animal egg.

3. So-called double fertilization is probably constant in Cypripedium. The primary endosperm nucleus (triple-fusion nucleus) is formed by the fusion of the polar, one synergid, and one male nucleus. Endosperm of four nuclei was found and the probability of other divisions taking place was noted.

4. In the presynaptic nucleus there is an evident pairing of the threads, probably of paternal and maternal origin. The gametophyte number of chromosomes is eleven, the sporophyte number is twenty-two, and the endosperm number is probably thirty-three. Distinct spirems were often found in all fusing nuclei, forming in one instance before contact. From these examples, the possibility of two spirems always forming in the sporophyte nucleus is suggested; this would secure the independence of the chromatin, and the fusing in synapsis would permit whatever exchange and mingling of parts there may be.

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EXPLANATION OF PLATES XXIV–XXVII

All figures were made with Bausch and Lomb camera lucida; *figs. 31* and *46* with Leitz no. 2 ocular and no. 7 objective; *figs. 61* and *62* with no. 4 ocular and no. 7 objective; all others with Leitz no. 4 ocular and B. and L. $\frac{1}{12}$ objective; details were filled in with a Zeiss apochromatic ocular and 2^{mm} objective.

The abbreviations used are as follows: *c*, chalazal daughter cell and nucleus; *e*, egg; *em*, embryo; *end*, endosperm; *g*, generative nucleus; *gc*, generative cell; *m*, micropylar daughter cell and nucleus; *meg*, megaspore nucleus; *p*, polar nucleus; *pe*, primary endosperm nucleus; *s*, synergid; *t*, tube nucleus; ♂, male nucleus.

PLATE XXIV

FIG. 1. *C. spectabile*. Ovule with mother cell in synapsis.

FIG. 2. *C. parviflorum*. Mother cell with well-organized spirem showing distinct chromomeres.

FIG. 3. *C. spectabile*. Nucleus of mother cell, with a few threads showing beginning of pairing.

FIG. 4. *C. candidum*. Pairing of threads very evident throughout the nucleus, but only a few threads shown.

FIG. 5. *C. spectabile*. Synaptic knot forming; pairing of threads evident.

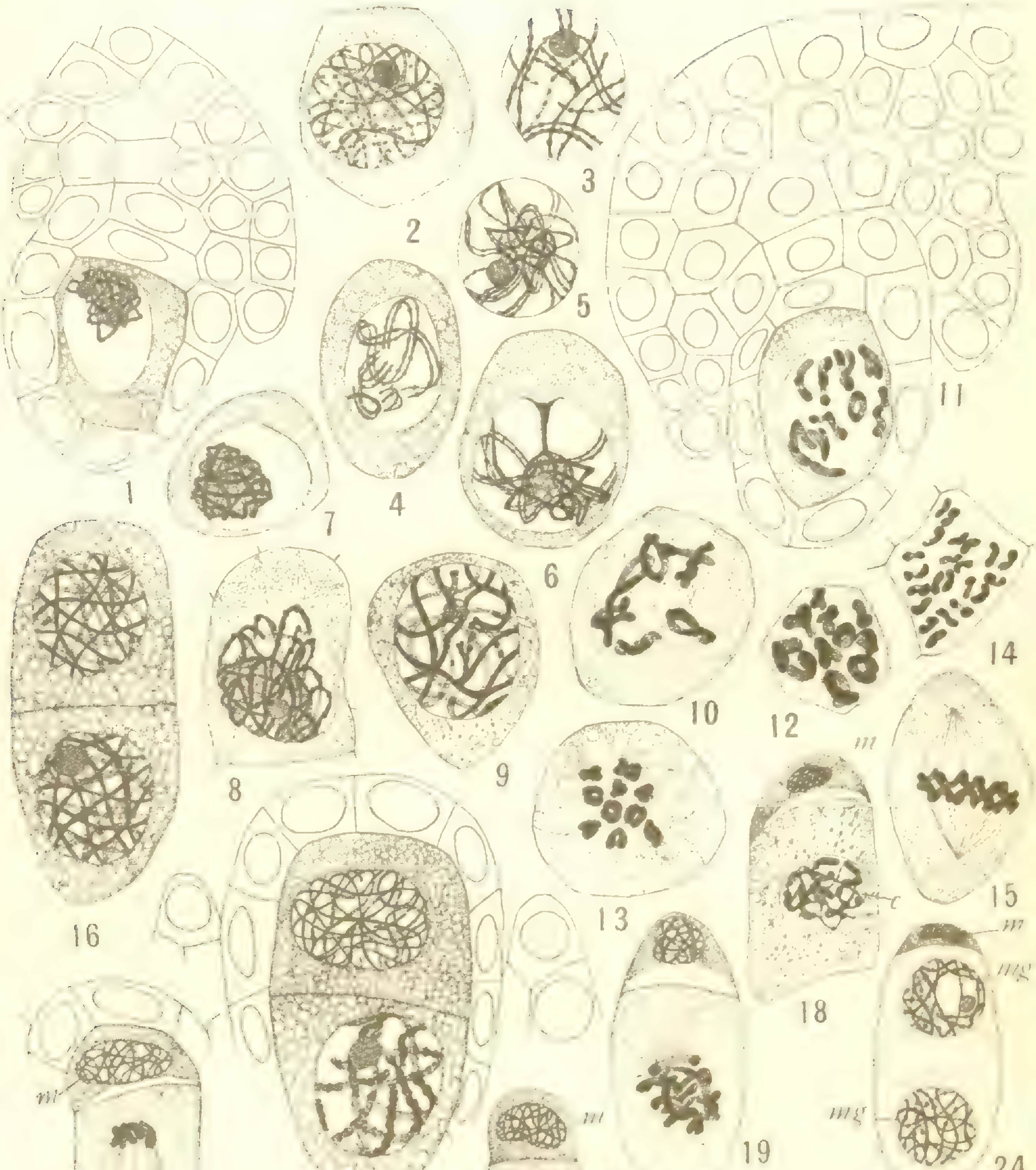
FIG. 6. *C. parviflorum*. Synaptic knot further advanced; threads in pairs and seemingly attached in places to nuclear membrane.

FIG. 7. *C. pubescens*. Synaptic knot complete.

FIG. 8. *C. spectabile*. Recovery from synapsis; lines of cytoplasm suggest multipolar spindle.

FIG. 9. Same. Shortening of thread; double nature evident at cut ends; lines of cytoplasm probably related to spindle formation.

FIG. 10. *C. pubescens*. Chromosomes formed.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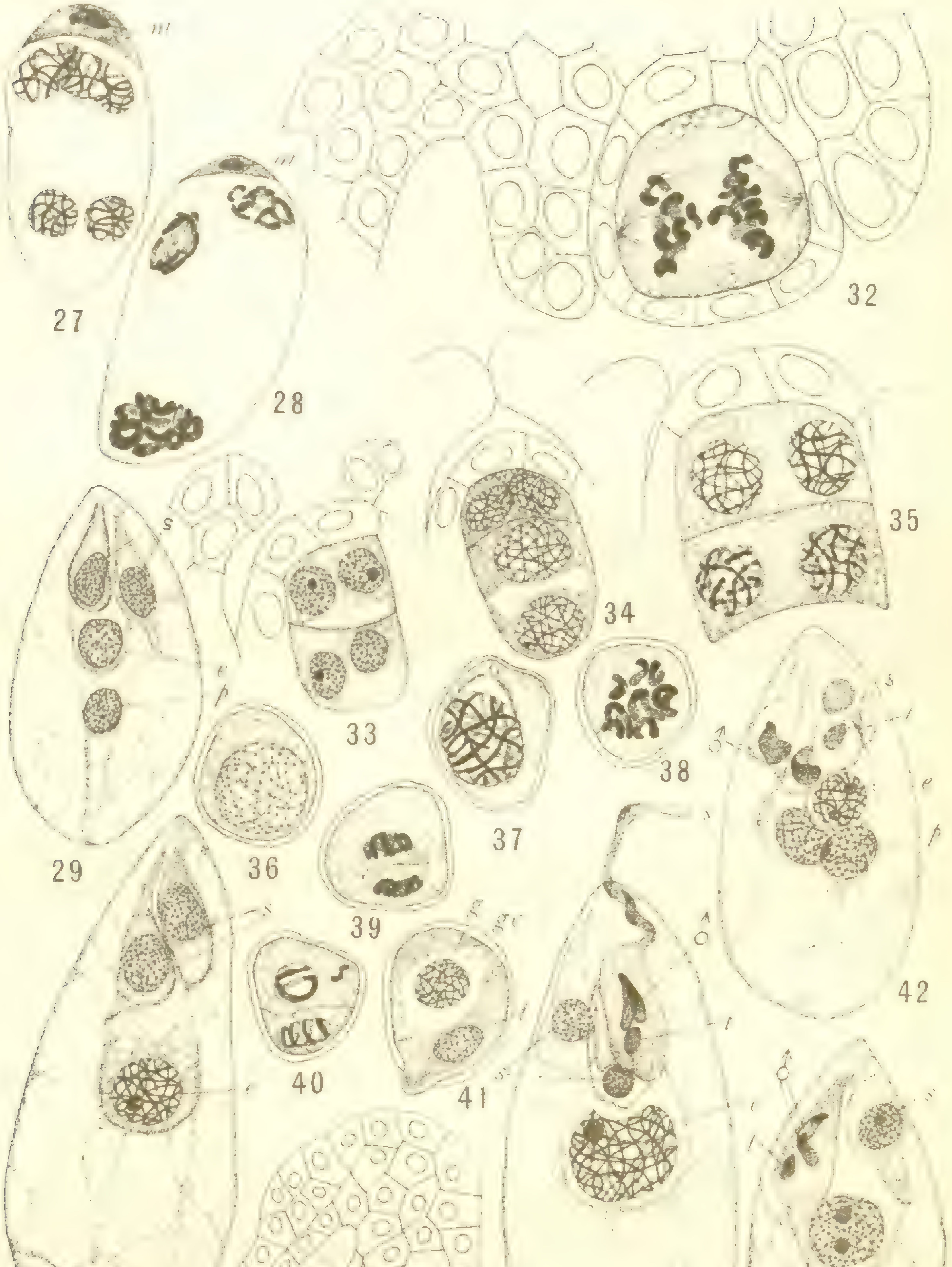
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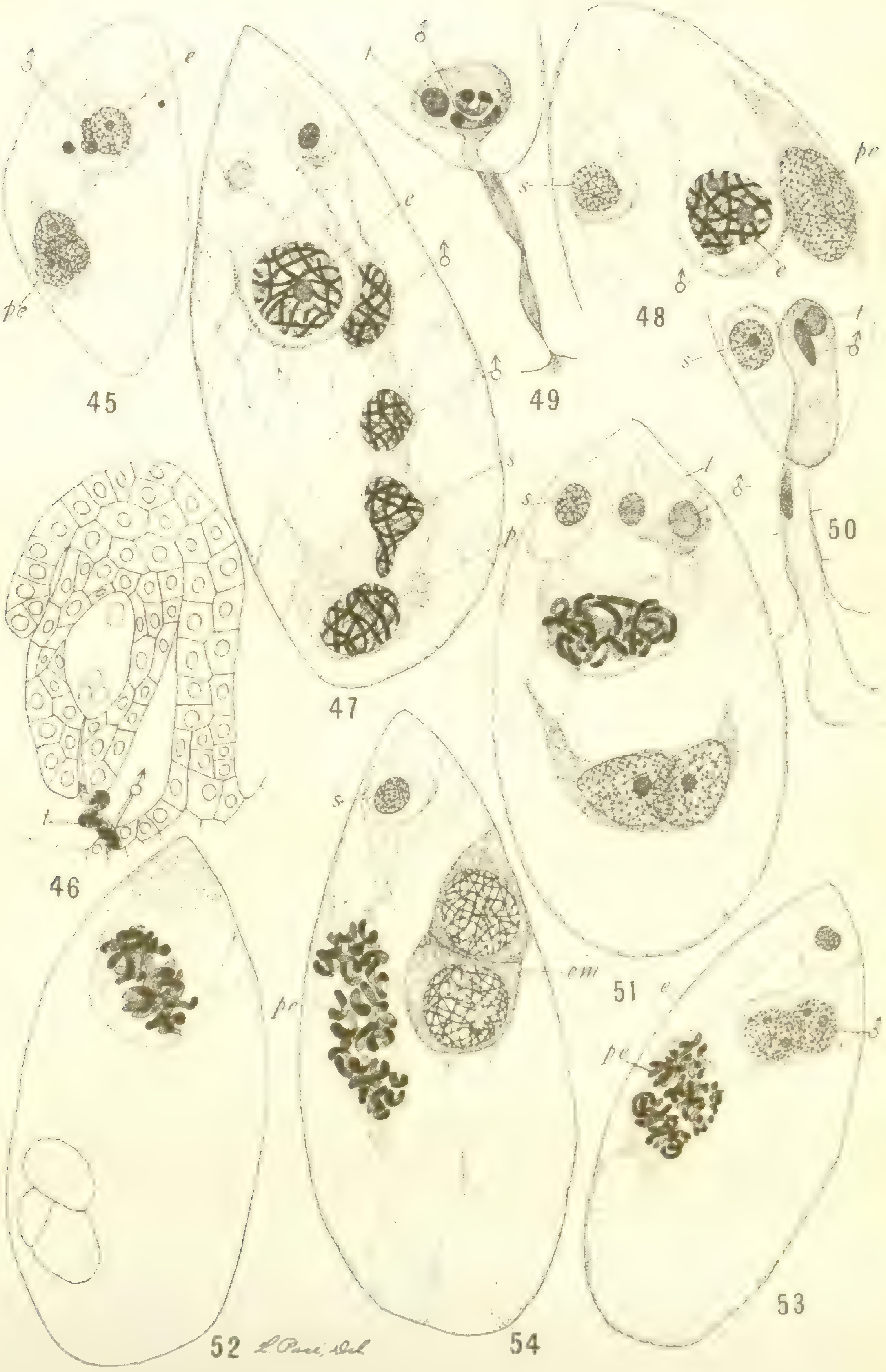
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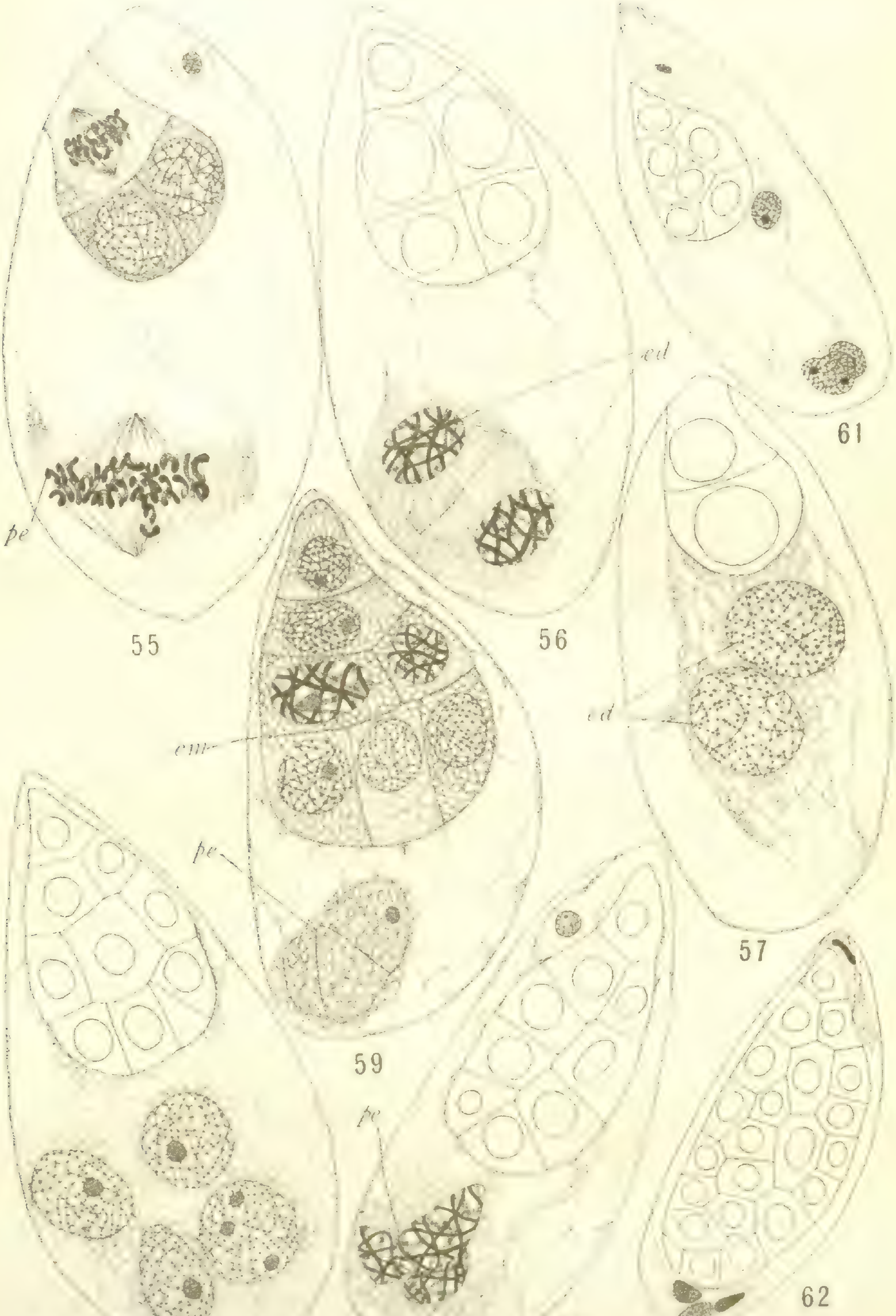
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FIG. 11. Same. Ovule with mother cell in late prophase or in metaphase; origin of spindle indicated by lines of cytoplasm.

FIG. 12. Same. Eleven chromosomes.

FIG. 13. *C. spectabilis*. Eleven chromosomes.

FIG. 14. Same. Wall cell of ovule showing twenty-two chromosomes (sporophyte number).

FIG. 15. *C. pubescens*. Typical spindle of mother cell.

FIG. 16. *C. spectabile*. Daughter cells formed by division of mother cell.

FIG. 17. *C. pubescens*. Daughter cells, with chalazal nucleus farther advanced than the micropylar.

FIG. 18. *C. spectabile*. Suggestion of bipolar spindle.

FIG. 19. Same. Metaphase of second division, longitudinal splitting of chromosomes.

FIG. 20. Same. Telophase of chalazal daughter cell; no indication of wall.

FIG. 21. *C. parviflorum*. Division of chalazal daughter cell complete; remains of spindle, but no evidence of wall.

FIG. 22. *C. spectabile*. Micropylar daughter nucleus developing and the chalazal one disintegrating.

FIG. 23. *C. parviflorum*. Division shown in *fig. 21* completed; the sac slightly enlarged and containing two megaspore nuclei.

FIG. 24. *C. spectabile*. Early spirem for the division of the megaspore nuclei; micropylar daughter cell still recognizable.

FIG. 25. Same. Spindles for division of megaspore nuclei; micropylar daughter cell still persists.

FIG. 26. Same. Four-nucleate sac; micropylar cell still undivided.

PLATE XXV

FIG. 27. Same. Four-nucleate sac, the nuclei differing in size.

FIG. 28. Same. Nucleus at antipodal end of sac in late prophase; the other in late telophase.

FIG. 29. *C. parviflorum*. Embryo sac ready for fertilization, showing egg apparatus and "polar" nucleus (near center).

FIG. 30. Same. Another view of sac, showing polar nucleus near antipodal end.

FIG. 31. Same. Two mother cells.

FIG. 32. *C. spectabile*. Spindle of mother cell at right angles to its usual position.

FIG. 33. Same. Four megaspore nuclei of equal size; no walls at second division.

FIG. 34. *C. parviflorum*. Four megaspore nuclei, as shown in *fig. 33*, but the inner pair the larger.

FIG. 35. C. *spectabile*. Four megaspore nuclei; traces of spindle showing, but no trace of wall.

FIG. 36. Same. Pollen grain; early spirem for division to tube and generative nuclei.

FIG. 37. Same. Later stage; "cap" showing orientation of spindle.

FIG. 38. Same. Pollen grain showing eleven chromosomes.

FIG. 39. Same. Telophase; wall forming.

FIG. 40. Same. Wall completed; a chromosome omitted in the organization of one of the nuclei.

FIG. 41. Same. Pollen grain developing tube.

FIG. 42. *C. parviflorum.* Pollen tube within the embryo sac.

FIG. 43. *C. spectabile.* About same stage as *fig. 42.*

FIG. 44. Same. Earlier stage; tube within sac and one synergid below it.

PLATE XXVI

FIG. 45. *C. parviflorum.* Double fertilization.

FIG. 46. Same. Ovule with tube just entering, having passed from ovary wall to micropyle.

FIG. 47. Same. Spirems formed in all the fusing nuclei before contact.

FIG. 48. Same. Spirems of male and female nuclei farther advanced than of the nuclei to engage in the triple fusion.

FIG. 49. Same. Pollen tube entering sac; male nuclei elongated and curved.

FIG. 50. *C. spectabile.* Pollen tube unusually broad; one male nucleus some distance behind the other.

FIG. 51. *C. parviflorum.* Segmentation of egg; two groups of chromosomes.

FIG. 52. *C. spectabile.* Segmentation of egg; two groups of chromosomes.

FIG. 53. *C. parviflorum.* Male nucleus and egg just in contact; late prophase of primary endosperm nucleus, which shows thirty-three (approximately) chromosomes in three groups.

FIG. 54. Same. Two-celled embryo; primary endosperm nucleus in late prophase and showing three groups of chromosomes.

PLATE XXVII

FIG. 55. Same. Spindle forming for division of primary endosperm nucleus; three- or four-celled embryo.

FIG. 56. Same. Telophase of division of primary endosperm nucleus; wall forming.

FIG. 57. Same. Endosperm of two nuclei and a two-celled embryo.

FIG. 58. Same. Endosperm of four nuclei.

FIG. 59. Same. Embryo well advanced; triple-fusion nucleus still distinct but in the resting stage.

FIG. 60. Same. Older embryo; triple-fusion nucleus in spirem stage.

FIG. 61. Same. Embryo of several cells; nuclei of the triple fusion not yet in contact.

FIG. 62. Same. Much older embryo; probably a triple-fusion nucleus, but no evidence of division.

GERMINATION OF SEEDS OF WATER PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 104

WILLIAM CROCKER

Various botanists have noticed peculiarities in the germination of the seeds of water plants. MÜLLER[1] found that the seeds of Eichhornia and Heteranthera do not germinate without first being desiccated, and LUDWIG[2] demonstrated this for the seeds of *Mayaca fluviatilis*. In commenting upon this PFEFFER says:[3] "Nor is it certain whether BRAUN and MÜLLER are correct in assuming that previous drying is essential for the further development of Chlamydomonas or for the germination of the seeds mentioned." Dr. LAND, of this laboratory, informed me in the autumn of 1906 that he had made various attempts to secure seedlings of Sagittaria and Alisma for class use, but had always failed except in one trial with Sagittaria. In that case a number of seeds grew after being left for a long period on wet soil in a hot greenhouse. At that time I began looking into the cause for the failure to germinate and had arrived at the main conclusion of this paper when an article by FISCHER[4] appeared on the subject.

The main points of FISCHER's paper may be stated briefly: The seeds of *Alisma Plantago*, *Potamogeton lucens*, *P. pectinatus*, *Hippurus vulgaris*, *Polygonum amphibium*, *Scirpus lacustris*, *S. maritimus*, *Sagittaria platyphylla*, *S. sagittifolia*, and *Sparganium ramosum* may be kept for years in water that is free from fermentation without germinating. If fermentation is set up in the water, germination soon begins. Germination can also be brought about, especially in Sagittaria, by subjecting the seeds to the action of bases and acids. FISCHER holds that the H^+ or OH^- ions act as stimulants on the dormant protoplasm of the embryo, arousing it to growth. He holds that the action is not on the coats, and adduces as evidence the facts that the seed coats are permeable to both water and compounds dissolved in it, and that a disorganization of the coats is brought about only by long exposure to such agents as concentrated H_2SO_4. He believes that the weak acids and bases used as stimuli could have no effect on the coats, and that in nature the germination is brought about by acid, formed in the decay of organic matter in ponds, which acts upon the dormant protoplasm.

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[1] See LUDWIG's article below.

[2] LUDWIG, F., Ueber durch Austrocknen bedingte Keimfähigkeit der Samen einiger Wasserpflanzen. Biol. Centralbl. **6**:299, 300. 1886.

[3] PFEFFER, W., Physiology of plants (Eng. ed.) **2**:210. 1903.

[4] FISCHER, ALFRED, Wassertoff- und Hydroxylionen als Keimungsreize. Ber. Deutsch. Bot. Gesells. **15**:108–122. 1907.

I find that FISCHER is entirely wrong in assuming, first, that the protoplasm of these seeds is in a dormant stage; and, second, that a chemical stimulus is necessary to bring about germination. Likewise MÜLLER is wrong in assuming desiccation to be necessary for the germination of the seeds of Eichhornia. I find that the embryos of all seeds of water plants I have tested begin germination very readily when the ordinary conditions for germination are furnished them, and especially the one condition of sufficient water supply. In an article already published,[5] I have shown that cases of delayed germination or entire failure to germinate are generally related to the character of structures inclosing the embryo and not to dormancy of its protoplasm. In the paper cited I mention certain species of Iris that germinate only when the cap covering the embryo is removed, although the structures are permeable to water and the embryo imbibes water until it entirely fills the cavity it occupies. The water thus admitted is not sufficient to start growth, and the embryo lies in this semi-saturated condition. It is only when the limits to water absorption are removed that growth begins. Exactly the same thing occurs with the seeds mentioned by MÜLLER and FISCHER. Before discussing this point farther some facts about the ripening and harvesting of the seeds mentioned in the table below must be stated.

The seeds of Alisma, Sagittaria, and Typha all ripen above water, while those of Eichhornia and Potamogeton ripen under water, as do the seeds of many other water plants. The ripening under water is brought about by the flower stalks responding positively to gravity soon after fertilization. A large number of Eichhornia seed stalks were gathered on October 1, while yet green, from one of the lagoons of Washington Park. Some of the green seeds were removed from the capsules and placed in distilled water, which was changed twice a day and kept at 23°C. Within a week twenty per cent. had germinated. A portion of the seed stalks were placed in distilled water repeatedly changed and kept at 23°C. Many of these seeds germinated while yet green and in the capsules. Still other seed stalks were kept in distilled water in an ice-chest at 6°C. None of these seeds germinated, but after three weeks many had ripened, as indicated by the hard brown coats. When the seeds with mature coats were kept at either 23° or 29° none germinated. Likewise seeds of *Potamogeton natans* and *P. pectinatus*, when gathered green and put into distilled water at 23° C. which was repeatedly changed, gave a considerable percentage of germination, while seeds allowed to ripen in the cold water of the ponds and then kept at 23° or 29° did not germinate.

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[5] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZETTE 42:265–291. 1906.

If the real conditions demanded for the germination of the embryos of these seeds are to be determined, the embryos must be freed from any possible effect of the coats by carefully rupturing them without injuring the embryos. An experiment, the results of which are embodied in the accompanying table, shows conclusively the effect of the coats on germination, as well as the true condition of the embryos as to dormancy. Ripe seeds were used in this experiment. To guard against any possibility of acid formation by fermentation, the seeds of Potamogeton were entirely freed from the fleshy material surrounding the hard seed coat, all were sterilized in five per cent. formalin for eight minutes, and then washed thoroughly in sterilized distilled water. The coats of one-half the seeds of each species were broken, with sterilized instruments, at the point where the cotyledons naturally emerge from the coats. This is a very tedious process, because the seeds are so small (especially those of Sagittaria, Typha, and Alisma), and because great care must be taken not to injure the embryos. After this treatment the seeds were put into sterilized distilled water and placed in a bath at 29°C. During the first two days they were kept in total darkness and after that in diffuse light. Within an hour after the coats were broken the cotyledons projected considerably, on account of the rapid imbibition of water. In one day germination was well started, as shown by the length of the cotyledons and their response to gravity. In two days the growth was very marked.

It might be urged that breaking the coats leads to increased oxygen supply and for that reason brings about germination. This is not at all probable for two reasons: first, increased oxygen pressures never bring about germination when the coats are intact; and second, these seeds require very little oxygen for germination. If the coats are ruptured, they will germinate if placed in water that has been previously boiled and covered with liquid paraffin. That the coats hinder germination by limiting the water supply is made evident by the fact that the cotyledon begins to project beyond the coat very soon after the latter is ruptured. In this experiment it seems impossible to justify the assumption that the protoplasm is in a dormant state or that the application of any external ions are necessary to start germination.

It is of interest to determine what structures surrounding the embryos limit the water absorption. In Sagittaria and Alisma there is an outer husklike exocarp and an inner hard endocarp. The removal of the exocarp did not increase the per cent. of germination, provided the endocarp was not injured in its removal. In Eichhornia the embryo is surrounded by a rather thick endosperm which is covered by a hard, fluted, brown seed coat. If the coat is broken at the side, it leads to a rather slow germination of over 50 per cent. of the seeds. If the coats are ruptured where the cotyledons naturally push out and where they lie very near the coats, nearly 100 per cent. germinate with remarkable promptness. This leads one to conclude that the hard coat chiefly limits water absorption, but that the endosperm too retards it. In the Potamogetons it is the hard stony coat that limits water absorption.

If the seeds of Sagittaria or Alisma are run through a coffee mill, set rather close, and are then placed in water, a large per cent. will grow. This breaks the seed coats without a very marked injury to the embryos. These seeds will also germinate after considerable time if planted in rich humus that is decaying by reason of abundant moisture and high temperature.

In the light of the work of MÜLLER and FISCHER two questions

Species	Condition of Coats	After 1 Day		After 2 Days		After 10 Days	
		Per cent. of germ.	Length of plantlets in mm.	Per cent. of germ.	Length of plantlets in mm.	Per cent. of germ.	Size of plantlets
Alisma Plantago........	Entire	0		0		0	
	Ruptured	86	2–3	86	3–7	98	2 leaves
Eichhornia............	Entire	0		0		0	
	Ruptured	96	2–4	98	4–7	98	2 leaves
Polygonum amphibium..	Entire	0		0		0	
	Ruptured	81	2–3	85	4–7	85	20–25^{mm}
Potamogeton natans*...	Entire	0		0		0	
	Ruptured	42	3–5	51	5–8	51	20–30^{mm}
Potamogeton pectinatus*	Entire	0		0		0	
	Ruptured	47	2–4	53	4–7	53	12–16^{mm}
Sagittaria variabilis.....	Entire	0		0		0	
	Ruptured	92	2–3	92	4–7	92	2 leaves
Typha latifolia.........	Entire	0		0		0	
	Ruptured	85	2–4	89	4–8	89	2 leaves

* The low percentage of germination here is due to many of the seeds having no embryos.

demand answer. How does a period of desiccation bring about the germination of the seeds of Eichhornia as shown by MÜLLER, or of Potamogeton as shown by FISCHER? What was the rôle of the bases and acids in FISCHER'S experiments? My experiments indicate that drying followed by soaking causes a considerable per cent. of the coats of Eichhornia to crack along the flutings, while it causes the rupture of the coats of Potamogeton along two creases that lie at the convex side of the embryo. Just how the bases and acids work has not yet been determined. That FISCHER is wrong in assuming that they arouse the dormant protoplasm is evident, for I have shown that the embryos respond to ordinary germinative conditions almost, if not quite, as readily as any embryos to be found. The action that causes the germination must evidently be upon the structures surrounding the embryos. That H^+ and OH^- ions, as well as many others, may increase somewhat the rate of growth of the naturally rapid-growing embryos, is not at all improbable. The fact that the coats showed no visible change when treated with acids and bases does not indicate that the coats were not radically changed. I have found that the impermeable coats of many of the seeds of the Leguminosae are made permeable by soaking them in absolute alcohol, and yet no change visible with the microscope appears. Experiments are being conducted now to determine the exact effect of acids and bases upon the seed coats and embryos of these seeds, as well as to determine in detail various other points connected with this problem.

I wish to emphasize again, as I have done already in the paper cited, the fact that delayed germination or failure to germinate is more generally due to seed-coat effects (limiting or entirely excluding water or oxygen supply) than to embryo characters, as has generally been assumed. On the other hand, in the same paper, I have shown that the failure of the seeds of hawthorns to grow under ordinary germinative conditions is due to embryo characters, and I have further stated that other seeds probably belong to this category. If seed coats play such an important part in failure to germinate, it is probable that spore coats act similarly in many cases. This hypothesis is now being tested.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

NOTES ON TWO CALIFORNIA NEMOPHILAS

NEMOPHILA MENZIESII var. **annulata**, var. nov.—Plants slender, prostrate, very brittle: cotyledons with oval blade and slender petiole: leaves rather less divided than in *N. Menziesii,* mostly 5-lobed, the upper greatly reduced but showing less tendency to become entire than in the variety *integrifolia* Parish: peduncles usually twice or more exceeding the leaves, often flexuous: flowers usually about or rather less than 1^{cm} across; calyx-lobes obtuse; corolla pale blue to almost white, with a deep-purple irregular ring above the scales, seldom dotted or hairy toward the center within; scales from 0.2 to 1^{mm} long, attached by one whole side or free at the tip (seldom as much as half free), ciliate with stiff bristles, which are often as long or longer than the scale is wide.

This variety is distinguished from the type by the greatly reduced size, lighter color, and peculiar markings of the corolla; the fewer-lobed, smaller leaves; the oval cotyledons; and the more delicate habit. From the variety *integrifolia* it is distinguished by the smaller size and the markings of the corolla; the lack of hairs within the corolla; the somewhat longer peduncles; the rather more divided leaves; and especially bv the corolla scales (cf. note to *N. Menziesii integrifolia,* BOT. GAZETTE **34**:205. 1902).

This is the first Nemophila reported from the desert regions of California. It was found among rocks at Dead Man's Point, near Victorville, on the Mojave desert. The type collection is Hall and Chandler, no. 6769, and the type specimens are in the herbarium of the University of California.

NEMOPHILA MENZIESII var. **rotata** (Eastw.), comb. nov.—Very close to the variety *integrifolia* Parish, with which I united it in my Revision of the Genus Nemophila (BOT. GAZETTE **34**:194). The examination of more abundant material seems to justify the retention of the form as a separate variety. It differs from the variety *integrifolia* chiefly in the smaller flowers (usually less than 1^{cm} across), which are usually of much deeper blue and nearly or quite rotate. The sinuses of the corolla are comparatively deep and the lobes comparatively narrow. The scales are oblong-linear, deeply laciniate, and attached by the narrow base only. So far as seen, the corollas were not dotted toward the center, but were covered with long hairs at the base within.

The range of this variety seems to be restricted to the vicinity of San Diego, California, the plants of ORCUTT from Lower California cited by

Miss EASTWOOD in connection with the original description being probably *N. pedunculata* Dougl. This opinion was ventured in my revision, though at the time that was written the Lower California locality seemed to be far beyond the known range of *N. pedunculata*, which had not been found south of the Santa Inez Mts. Since then, however, I have found the species at Witch Creek, San Diego County, so that it may easily range into Lower California.—HARLEY P. CHANDLER.

BRANCHING SPORANGIOPHORES OF RHIZOPUS

(WITH ONE FIGURE)

Current texts agree in stating that the sporangiophore of *R. nigricans* bears a single sporangium. For example, SWINGLE states[1] that "each sporangiophore bears a single spherical sporangium." In a recent culture on bread, some two weeks old, two anomalous conditions were observed (*fig. 1*). In one case, by two successive branchings, one sporangiophore bore three normal sporangia. In the other case, by a single dichotomous branching, two sporangia were developed.—LEROY H. HARVEY, *Yankton College, Yankton, S. D.*

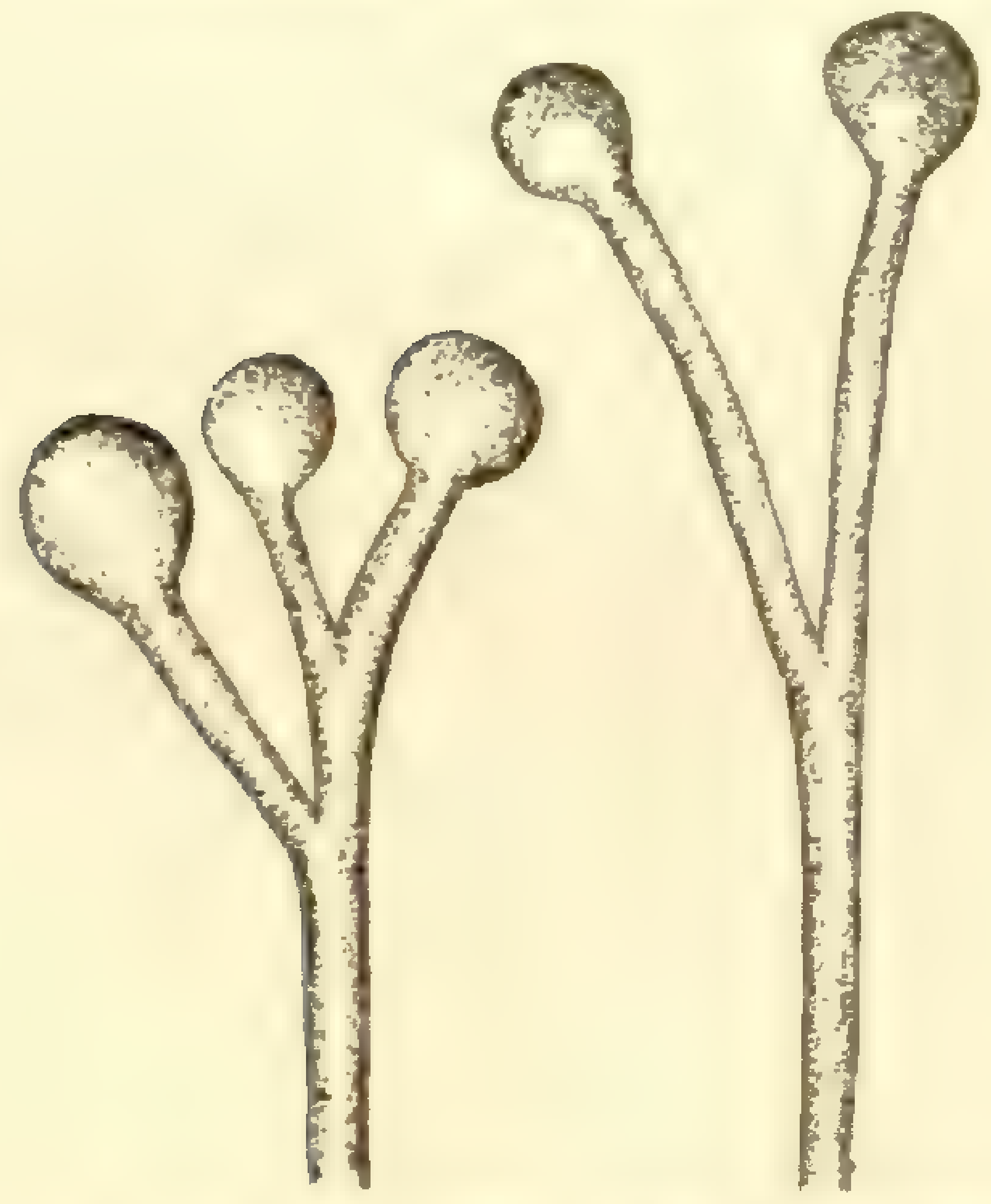

Fig. 1.—Branching sporangiophores of Rhizopus.

AN UNUSUAL METHOD OF VEGETATIVE REPRODUCTION IN *DIONAEA MUSCIPULA*

(WITH ONE FIGURE)

In 1892 I described and illustrated an abnormal development of the inflorescence of Dionaea.[2] Two years ago I found an exactly similar kind of growth in a number of plants which had been kept in pots on a shelf next to the glass of a greenhouse with a southern exposure. In the axils of the bracts were found short vegetative branches, each with a number of perfect fly-traps (*fig. 1*), which closed when any of the six hairs on their upper surface were touched twice in succession. The response, however, was of the most sluggish character. The plants, when full grown, were rather crowded together by the arrangement of the pots, and whether this crowding induced the formation of the upper leafy branches I am unable to state. In the paper above mentioned, I suggested that "it might have been possible to have grown new individuals from the axillary vegetative branches, but the suggestion of this idea came after the plant had been killed and preserved in alcohol."

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[1] Bureau Pl. Industry Bull. 37. 1903. p. 15.

[2] HARSHBERGER, JOHN W., An abnormal development of the inflorescence of Dionaea. Contrib. Bot. Lab. Univ. Penn. 1:45–49. *pls. 5, 6.* 1892.

As a considerable abundance of material was provided by the abnormal growths produced two years ago, I cut off a number of the short leafy inflorescence branches and placed them in a sand bed used for the propagation of cuttings and covered with a hinged glass door. In ten days or two weeks after these interesting branches had been placed in the sand, they had developed, some one, others as many as four or five secondary roots, that had reached a length of one or two inches, when the plants were removed and placed in alcohol. The new plants, thus obtained by vegetative propagation, grew rapidly in the size of their leaves and were perfectly healthy and normal in structure. Thus, I verified the supposition made thirteen years ago that Dionaea can reproduce itself vegetatively by means of leafy branches proliferated in place of the inflorescence branches.—JOHN W. HARSHBERGER, *University of Pennsylvania.*

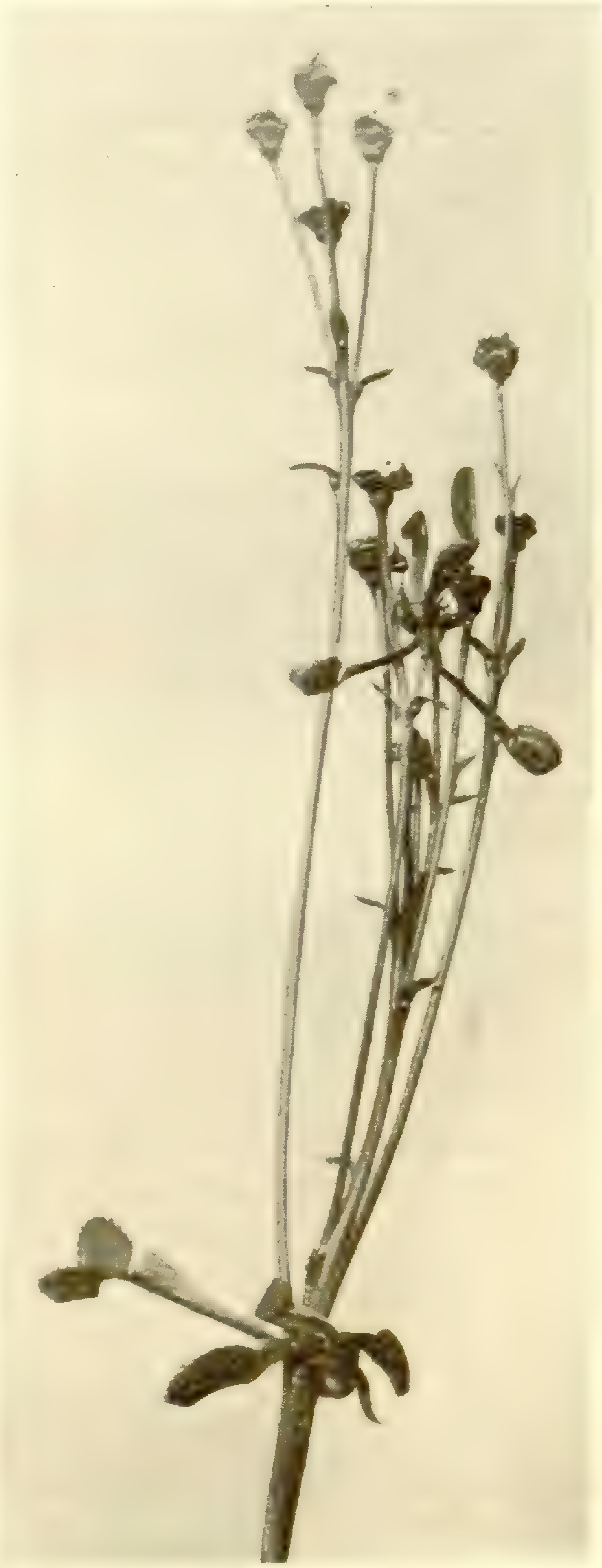

FIG. 1.—Dionaea muscipula.

CURRENT LITERATURE

BOOK REVIEWS

Handbook of trees

Many attempts have been made to bring into popular form such descriptions of our trees as would enable the amateur to recognize the various species at different seasons. It has remained for Mr. ROMEYN B. HOUGH to produce a book that adequately accomplishes this laudable purpose.[1] But it does much more; it brings to the forester, lumberman, cultivator, and botanist alike such a compact and comprehensive portrayal of the trees of the northern states and Canada as has never before been at his service.

As publisher of the well-known *American woods*, Mr. HOUGH has been much in the field and has thus had opportunity to make the notable collection of photographs which make this *Handbook* unique. He has not been satisfied with photographs of less than the highest quality. His pictures of leaves and fruits stand out, without distracting shadows, on a background ruled in 1-inch squares, showing at a glance the relative size, whether the original print is much or little reduced in making the fine half-tones for the book.

Each of the 208 species is illustrated by a full-page plate showing a branchlet with leaves and fruits, the latter usually dissected to show the seeds, and a twig in winter condition; a cut about 2×5 inches, showing a medium-sized trunk, with the normal appearance of the bark; and a small map of the United States and British America showing by shading the distribution of the species. In many cases there is in addition a cut about 2 inches square, showing a thin transverse section, magnified 15 diameters, which would often enable one to identify a doubtful piece of wood. These figures, admirably engraved and printed, are set on two facing pages, and in the small remaining space there is a letter-press description of the species, both diagnostic and general. At the end there are analytic keys and a glossary.

We cannot think of an item which would contribute to greater completeness. Everything that has been attempted seems to have been well planned and well executed. The basis of nomenclature is not stated; but synonyms in "recent works" are given. Of course much depends upon the accuracy of Mr. HOUGH'S identifications, but his long experience and the cooperation of other dendrologists ought to insure that. The book may be commended as indispensable for public and school libraries, for all students of trees, and for botanical laboratories. Considering the labor it represents and the wealth of illustration, the price is reasonable.—C. R. B.

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[1] HOUGH, R. B., Handbook of the trees of the northern states and Canada east of the Rocky Mountains. Photo-descriptive. 8vo. pp. x+470. *figs. 498*. Lowville, N. Y.: The Author. $8.00.

Pavia memoirs

The tenth volume of the *Atti* of the botanical institute of the University of Pavia[2] precedes in publication the ninth, because the plates of an incomplete research are already printed and numbered for the ninth volume. Volume X, containing work dating from 1904 to 1907, opens with a portrait of Federico Delpino, a bibliography, and a brief dedication of the volume to him by his friend, the director, Dr. Giovanni Briosi.

There are several papers on plant diseases. First is an elaborate and well-illustrated account by Briosi and Farneti of the white rust of the lemon, a serious disease in Sicily, due to some of the developmental forms of *Rhynchodiplodia Citri*, such as *Pseudofumago Citri*, *Cladosporium Citri*, *Hormodendron Citri*, etc. Turconi describes a new fungus from Mexico, *Phyllachora mexicana*, parasitic on *Adolphia infesta* Meissn., the *chaquirilla*. Farneti and Pollacci describe a new mode of dispersal of phylloxera by hibernating larvae, inclosed in galls of peculiar form. Farneti has a paper on a disease of rice, known in Italy as *brusone* and by a great variety of other names, which he ascribes to a single rather polymorphic fungus, *Piricularia Oryzae* Briosi & Cavara. It occurs also in Japan. It is transmitted by infected seeds and straw, and spores are distributed by wind and water. The parasite infests Panicum and Leersia also. Briosi details his rather hurried observations on the government nurseries of vines in Sicily, in which the disease *roncet* has appeared among the American stock destined to replace the vines destroyed by phylloxera. The disease is not threatening, but he recommends precautions. Besides these there are various short notes on fungus diseases.

There are several microchemical papers; one by Cazzani is a critique of Goris' work on esculin; another by Pollacci suggests a better mode of testing for phosphorus in plant tissues. Pollacci also reviews the history of the discovery of formaldehyde in plants and files his *caveat* as first discoverer in July 1899.

In physiology there are three papers. One is a short note by Montemartini, bringing evidence against Jost's theory that the development of the leaf traces is due to stimulus from the growing organ above. A paper by the same author gives a résumé of the previous work upon the formation of proteids and reports the first results he obtained in a study of the effects of light on the process, which indicate that it is favorable thereto. Pollacci, confirming his earlier conclusions, reports that plants emit hydrogen in light; but he also finds that they give it off in darkness, and that certainly cannot be related to photosynthesis. Nevertheless he maintains the reduction of H_2CO_3 by H_2 into $HCOH + HOH + O$.

The morphological papers include two brief notes by Montemartini, one on the origin of anomalous pitchers from the leaves of *Saxifraga crassifolia;* the other on a biological adaptation of the leaves of *Buxus sempervirens*, wherein he finds a mass of ice formed on freezing days between the lower epidermis and the mesophyll, which, he says, protects the leaf from further harm by cold and serves by retaining the water (ceded later to the stems) to facilitate the development of buds in spring!

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[2] Atti dell' Istituto Botanico dell' Università di Pavia. Redatti da Giovanni Briosi. II Serie, Volume X. Imp. 8vo. pp. xxiv+361. *1 portrait. pls. 28* (20 colored). Milano: Tipo-Lit. Rebeschini di Turati E. C. 1907.

The most voluminous morphological paper is one by BUSCALIONI and TRAVERSO on the morphological evolution of the flower in relation to the chromatic evolution of the perianth. They seek to show that the evolution of floral coloration is neither due merely to insect relations nor is it monophyletic. At least two lines are recognized, one characterized by the dominance of the xanthic series, the other by the cyanic. "Internal causes" primarily, then insect visits and "other factors," have been the agents in modifying the first flowers, which they assume to have been anemophilous—an assumption that needs defense. Of course "inherent causes" is simply a confession of defeat. HENSLOW'S theory (1893) came to their attention only after part of the work was printed; his book on *The origin of floral structures* is critically discussed in an appendix, and his theory mildly approved.

The volume closes with official reports of the work of the Royal Cryptogamic Laboratory of the Institute in 1904 and 1905. They show that it is doing good service for the country and the various researches indicate the activity and energy of the staff.—C. R. B.

Progress of botany

In the second part of the first volume of this admirable series, CZAPEK gives a résumé of the progress of our knowledge of the nutrition of plants since the publication of the first volume of PFEFFER'S *Physiologie*.[3] By his interpretation *Ernährungsphysiologie* covers even more than our blanket-word metabolism; for he discusses the mechanics of all the exchanges of material between the plant and the outer world, and the movement of water and foods within it, as well as the synthesis of foods, their assimilation, the non-plastic products, the ash constituents, enzymes and cytotoxins, respiration, and fermentation.

To do this within 114 pages would not be possible, were it not that the author can refer in many places to the summary already prepared in his *Biochemie der Pflanzen*. It must be remembered that a reporter sees things from a particular angle, and while we cannot always approve the point of view occupied by this author in surveying the field of research, we do recognize his synopsis as comprehensive and complete. It is especially useful in its inclusion of investigations carried on in eastern and southeastern Europe, that unfortunately are too often overlooked by the more western peoples, either through carelessness or unfamiliarity with the Slavic languages.

So much is included in CZAPEK'S summary that would hardly be expected even from the topics named, that it behooves every physiologist to read this paper and have it at hand for reference.—C. R. B.

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[3] CZAPEK, FRIEDRICH, Die Ernährungsphysiologie der Pflanzen seit 1896. Progressus Rei Botanicae (ed. J. P. LOTSY) 1:417–532. Leipzig: Gustav Fischer. 1907. Per volume, *M* 18.

MINOR NOTICES

Gulf biologic station.—This station was established in 1903 by the state of Louisiana at the mouth of the Cameron River. The region is about at sea-level and practically treeless, the station itself being on a ridge running parallel to the sea and traversing a salt marsh. The plants of this very interesting locality have been published in a catalogue prepared by R. S. COCKS.[4] In addition to the list of species of the immediate vicinity, there are notes on certain species of the prairie region of southwestern Louisiana.—J. M. C.

Das Pflanzenreich.[5]—Part 29 contains the Erythroxylaceae by O. E. SCHULZ. After the usual preliminary account of literature, general characters, anatomy, geographical distribution, etc., the synopsis of the family is presented. Besides the monotypic genus Aneulophus, the family contains only the large genus Erythroxylum, which is credited with 193 species, 41 of which are described as new. The author breaks up the genus into 19 sections, to each of which a name is given.—J. M. C.

Key to trees and shrubs.—COULTER and DORNER[6] have published a convenient untechnical key to the genera of trees and shrubs of Indiana and the neighboring states, based chiefly upon leaf characters. A previous edition, now exhausted, was restricted to the forest trees, but the value of the present edition is much increased by including the shrubs.—J. M. C.

NOTES FOR STUDENTS

Mendelian inheritance.—DAVENPORT[7] in a lecture before the Washington Academy of Sciences discussed Mendelian inheritance in the light of his studies on poultry. After saying that "expectation has been so often realized that MENDEL'S law has gained deserved fame as the most important law of inheritance yet enunciated," he proceeds to give a few non-conformable cases, and concludes that there must be some more inclusive law. This he calls the "law of potency," the gist of which may be given in his own words thus:"Between the two extremes of equipotency and allelopotency lies the great mass of heritable characteristics which when opposed in heredity exhibit varying degrees of potency." It is not clear why this should be called a law; it seems rather to be a denial that any law exists. Some cases similar to those cited have been found to conform with

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[4] COCKS, R. S., The flora of the Gulf biologic station. Baton Rouge: La. State Board of Agric. and Immigration, Bulletin 7. pp. 42. 1907.

[5] ENGLER, A. Das Pflanzenreich. Heft 29. Erythroxylaceae von O. E. SCHULZ. pp. 176. *figs. 32* (297). Leipzig: Wilhelm Engelmann. 1907. *M* 8.80.

[6] COULTER, STANLEY, and DORNER, HERMAN B., A key to the genera of the native forest trees and shrubs of Indiana. pp. 24. Lafayette: The Authors. 1907. 20 cents.

[7] DAVENPORT, C. B., Heredity and Mendel's law. Proc. Wash. Acad. Sci. 9:179–188. 1907.

Mendelian expectation upon keener analysis of the characteristics involved, and it seems early for the formulation of a law to accommodate exceptional cases until hypotheses are exhausted for making them conform to laws now so fully demonstrated as those of MENDEL. There is no necessity for the assumption that there is an all-inclusive law of heredity, and it seems probable that there may be a number of more or less independent laws of greater or less inclusiveness which separately or conjointly may explain each single instance of inheritance. Some evidence exists that "variable potency" may represent a fact, but so far as the evidence goes, this fact is of much smaller significance than the segregation of pure gametes. Indeed it is conceivable that variations in potency may be due to several or many different causes, and that it does not represent a sufficiently unified series of phenomena to warrant its designation as a law.

COOK[8] in discussing DAVENPORT'S lecture attempts to classify various methods of descent, and limits "Mendelism" to cases of complete dominance, quite ignoring the feature of Mendelism now everywhere recognized as the most important, namely, the segregation of pure gametes. In the literature of Mendelism valid explanations of phenomena have been given belonging to most of COOK'S categories, and it seems not unlikely that Mendelian explanation will be found sooner or later for the greater part of the phenomena which COOK classes under polar inheritance. The classification as well as the whole paper is academic and represents thinkable conditions rather than actual ones. He attributes polar inheritance, except in the case of dimorphic and polymorphic species, to narrow breeding, but this assumption is as yet unsupported by experimental evidence. The paper is full of misconceptions and misstatements, the recklessness of which is in places startling and amusing. "Elementary species" (p. 206) are wrongly defined as the different kinds or castes of dimorphic or polymorphic species, and "heterozygote" (p. 211) is incorrectly limited to those heterozygotes which display novelties, i. e., characters not found in the parents. The tendencies of the author to construct a peculiar terminology to represent his thought rather than follow accepted usage is shown in the use of "conjugate" with the same meaning as the word "zygote," now universally adopted by experimenters in this field. Failing to grasp the possibility that any character may be made up of two or more factors, he is led to the startling conclusion (p. 220) that it is possible for germ cells to transmit characters for many generations without bringing or tending to bring them into expression, and that the Mendelian "laws of disjunction," "purity of gametes," "alternative inheritance," or whatever they may be called, become at once superfluous and inadequate.

His statements regarding mutations are all academic and mostly without any experimental support. Thus, he says (p. 199), "If the narrow breeding be carried on with persistence, mutative reactions toward greater diversity will appear, and these sudden deviations from an established heredity are even more different than were the normally diverse individuals of the original species." Again (p. 220), "Mutative variations commonly obey MENDEL'S laws." But none of the fully demonstrated mutations now known strictly obey MENDEL'S law, though the reverse inference has been frequently made and probably with good cause, namely, that the Mendelian inheritance of a character indicates its origin by mutation. On p. 221 he says, "The general rule must be that new variant gametes conjugate with gametes of the unmutated parental type, and thus have from the first the reproductive status of Mendelian crosses." This is a good suggestion and should be kept in mind by students of evolution, as should also his discussion of the relation between the origin of characters and their effect in the modification of species; but the Oenothera mutants, the best known of all, breed true from the instant of their first appearance, and no instance is known in which a new form has been shown to be already a Mendelian hybrid at the time of its first appearance.

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[8] COOK, O. F., Mendelism and other methods of descent. Proc. Wash. Acad. Sci. 9:189–240. 1907.

It is difficult to understand why COOK should say, "Mutation is not a period but a condition," since no one ever said or intimated that it is a period. It is neither a period nor a condition, but an act or the result of that act. He says, "Species have more essential evolutionary differences than mutations, though mutations are at the same time more definitely different." Yet the Oenothera mutants are recognized by excellent taxonomists as differing from each other both as to quality and degree, just as wild species differ. Other statements regarding the Oenotheras are not in agreement with published facts, as for instance his statement that *O. Lamarckiana* is dominant over *O. lata* to the extent of 85 per cent.—GEORGE H. SHULL.

The origin of angiosperms.—ARBER and PARKIN[9] have proposed a theory of the origin of the angiosperms, based on the recent development of knowledge in reference to living and fossil forms, especially the Bennettitales. Contrary to the ENGLER scheme, they do not regard such apetalous groups as the Piperales, the Amentiferae, and the Pandanales as representing primitive angiosperms, but rather as reduction forms from those possessing a perianth. The primitive typical angiospermous floral structure is claimed to have been an "amphisporangiate" (substituted for the commonly used terms "bisporangiate" or "ambisporangiate," as the proper antithesis of "monosporangiate") strobilus, in which the megasporophylls are above the microsporophylls and there is a well-marked perianth. Such a strobilus the authors call an "anthostrobilus," restricting "flower" ("eu-anthostrobilus") to angiosperms. A "pro-anthostrobilus" is an earlier form, such as is displayed by the Bennettitales, in which the megasporophylls are not closed, and the microsporophylls have not reached the real stamen form. This implies the existence of a direct ancestral group of the angiosperms, with a strobilus like that of the Bennettitales, and to this hypothetical group the authors give the name "Hemiangiospermeae." To this hypothetical group the Bennettitales are related, but are specialized in their own way.

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[9] ARBER, E. A. NEWELL, and PARKIN, JOHN, On the origin of angiosperms. Jour. Linn. Soc. London Bot. **38**: 29–80. 1907.

The living angiosperms most nearly related to the "Hemiangiospermeae" are the Ranales, especially the Magnoliaceae, whose probable primitive position has begun to force itself upon the attention of morphologists ever since WIELAND'S studies of Bennettitales; and from this same Ranales plexus the monocotyledons probably diverged. The monophyletic origin of angiosperms is maintained, but to the reviewer it seems altogether probable that while a simple strobilus, like that of Bennettitales, resulted in such a flower as that of the Ranales, a compound strobilus, like that of the Gnetales, may have resulted in such an inflorescence as an ament.

An inevitable suggestion is that the pteridosperms developed in the Mesozoic by two distinct methods: (1) by sporophylls aggregated into monosporangiate strobili leading to the modern cycads; (2) by both kinds of sporophylls massed into one amphisporangiate strobilus, as in Bennettitales.

The paper contains many interesting and suggestive details which cannot be mentioned here, and it brings together in every useful form views which have been working like leaven, but which had not been expressed.

Another paper dealing with the method of origin of angiosperms, rather than with their phylogeny, is that by COOK.[10] It is a theoretical discussion of the possibility of angiosperms arising directly from liverworts, such as Anthoceros, through the persistent aposporous development of the prothallia, which serve "as means of attachment for the young plant during its embryonic stages." "Apospory need not interfere with the formation of sex cells, nor with the continuation of truly sexual methods of reproduction." It seems that in this elimination of spores "mitapsis" is simply deferred to later generations of cells, in angiosperms being carried over into the aposporous female prothallium. From an Anthoceros capsule an angiosperm with two cotyledons could be derived; and then a many-leaved stem could be built up by the successive addition of "metamers." The elimination of megaspores in the life-history of angiosperms results in such new interpretations of structure that the reviewer must confess he is unable to follow the discussion. For example, "the part of the angiosperm which, in the present view, might correspond to the prothallus itself, is the nucellus. And even this relation would not be direct, for the nucellus of the angiosperms might not be homologous with the nucellus of the conifers and cycads, which, if current interpretations are correct, is more analogous to the placenta of the mammal than to an aposporous prothallus." Also, "the gymnosperms may be supposed to have the ovules and seeds naked because they are still borne in an endosperm which corresponds to the primitive, vegetatively functional prothallus, though it now remains attached to the much more highly developed double-celled structure which corresponds, in turn, to the capsule of the liverwort and the moss, the frond of the fern, and the leafy axis of the club moss." When revolutionary ideas are combined with evident lack of familiarity with the structures under discussion, it is no wonder that confusion is the result.—J. M. C.

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[10] COOK, O. F., Origin and evolution of angiosperms through apospory. Proc. Wash. Acad. Sci. 9:159–178. 1907.

Development of heterotypic chromosomes.—Two years ago MOTTIER published a preliminary account[11] of his views as to the development of the heterotypic chromosomes in pollen mother cells, and the full paper has just now appeared.[12] His paper consists of two parts: first, a statement of the results of his studies of five angiosperms (*Podophyllum peltatum*, *Lilium Martagon*, *L. candidum*, *Tradescantia virginica*, and *Galtonia candicans*); and second, a discussion of several cytological phenomena, reviewing the work of previous investigators and giving a purely theoretical account of the possible relationships of chromosomes to hereditary characters.

The few points which he has specially emphasized in his own studies on these five forms are as follows: (1) The resting nucleus of the pollen mother cell consists of a linin net, the ground matrix in which the chromatin is held. The chromatin is in the form of very fine granules of uniform size or in larger aggregations or clumps which are composed of smaller granules. (2) In synapsis he has not found a union of two spirems. (3) The loose or hollow spirem which has emerged from synapsis is of the double nature, which he believes to be due to a new longitudinal splitting that provides for the second division. (4) Segmentation of this loose or hollow spirem into chromosomes takes place during or following the second contraction stage. The second contraction consists in the arrangement of a large part of the spirem into loops that tend to radiate from a loosely entangled central mass of the thread. The loops are formed by the approximation of the parallel portions of longer turns of the spirem. Each loop represents a bivalent chromosome, each parallel part being a single chromosome. The two parallel parts or chromosomes are arranged tandem, or end to end in the spirem. (5) He seems to emphasize the point that the shortening and thickening of the spirem occurs, in the main, after segmentation of the spirem into chromosomes.

Taking his results as a whole, they confirm essentially the view already advanced by FARMER and MOORE, SCHAFFNER, and STRASBURGER. His theoretical discussion starts from this point: he has never found the number of chromosomes to be represented by prochromosomes in presynaptic stage; all identity of such bodies is lost. He thinks granules in the resting nucleus should be connected with smaller units, the pangens (following the terminology of DEVRIES); and with a purely theoretical consideration of the pangens and their relation to chromosomes and to heredity, the paper closes.—S. YAMANOUCHI.

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[11] MOTTIER, D. M., The development of the heterotypic chromosomes in pollen mother cells. BOT. GAZETTE **40**:171–177. 1905.

[12] MOTTIER, D. M., The development of the heterotypic chromosomes in pollen mother cells. Annals of Botany **21**:309–347. *pls. 27, 28.* 1907.

Resting buds as indices of ecological types.—RAUNKIAER[13] has regarded the world of vegetation from a somewhat new view-point, and has developed some ideas that seem of great value. Prevailing ecological classifications have commonly divided vegetation into xerophytic, mesophytic, and hydrophytic groups, in which the foliage organs have been the dominant element. RAUNKIAER thinks that the most rigorous season to which a plant is subjected is the one which should show the most critical ecological structures. Hence he proposes a new classification, based on resting buds and other organs that are most in evidence in rigorous seasons. On this basis five great plant classes are recognized: phanerophytes, whose buds are considerably above the ground (trees and shrubs); chamephytes, whose buds are slightly above the ground; hemicryptophytes, whose buds are at the ground level; cryptophytes, whose buds are hidden in the ground; and therophytes, whose buds persist only in seeds (annuals). The phanerophytes, especially, may be much subdivided: according to size into mega-, meso-, micro-, and nanophanerophytes; according to leaf-fall habit into evergreen and periodically deciduous; according to bud structure into forms with naked or scaly buds. Chamephytes may have stems that are erect in favorable seasons, or stems that are always horizontal. Cryptophytes are divided into geophytes, helophytes (marsh plants), and hydrophytes; geophytes are further subdivided into rhizome, bulb, root-tuber geophytes, etc. The author remarks on the distribution of these various types in relation to soil and climate. It is his idea that the classification of plant formations can be more readily and scientifically accomplished by the recognition of the above types than on other lines. The reviewer feels that the contribution is of great value, and that perhaps RAUNKIAER has given us the most practical classification of vegetation forms we yet have. It seems a pity, however, that the paper is cumbered with so many new terms. For instance, why say therophyte for annual? Too often good ideas are buried under a ponderous Greek or Latin terminology.—HENRY C. COWLES.

Antitoxic value of complete and of incomplete foods.—LE RENARD[14] has undertaken to ascertain how *Penicillium glaucum* can grow in such concentrated solutions of the salts of copper, and also how the resistance of the organism to the toxic salt is modified by varying conditions of nutrition. The maximum concentration of four salts of copper (sulfate, nitrate, chlorid, and acetate) which will allow germination in the presence of complete and incomplete foods has been determined. A complete food contains the eight essential elements according to the empirical formula $C_6H_{12}O_6+NH_4NO_3+MgSO_4+KH_2PO_4+H_2O$. An incomplete food is one whose corresponding empirical formula is deficient. Fully one-half of the paper is devoted to literature, general biology, and physiology of Penicillium, together with a long discussion of the nature of toxicity.

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[13] RAUNKIAER, C., Types biologiques pour la géographie botanique. Bull. Acad. Roy. Sci. Lett. Danemark **1905**:347–437.

[14] LE RENARD, ALF., Essai sur la valeur antitoxique de l'aliment complet et incomplet. 8vo. pp. 1–211. Paris: J. Mersch. 1907.

The author draws thirty distinct conclusions, only a few of which can be noted here. A mineral salt used alone in normal or less than normal concentration does not increase the resistance of the fungus to copper salts, and therefore has no antitoxic value. Carbohydrates in the presence of a suitable mineral salt are antitoxic to an extent which for a constant quantity of that salt becomes zero at about centinormal for the aldoses, but reaches much lower for the ketoses and hexoses. The antitoxic action of a food seems to be correlated with a composition which includes a suitable carbon compound and a suitable mineral salt, united with an organic or a mineral acid. Such a combination the author designates a "complex" in which the toxin and the antitoxin are present in proportions which make a simple ratio representing a double compound (organo-metallic) which suggests by its composition and modifications the side-chain of EHRLICH. The germination of Penicillium in toxic solutions of copper is therefore to be attributed to the presence of such a complex. The paper is really an elaborate study of undoubted value, but the reviewer has not undertaken to digest the evidence for the conclusions enumerated.—RAYMOND H. POND.

Chemistry of fertilization.—LOEB'S address before the International Zoological Congress[15] is of general physiological interest. Summarizing all the experiments on artificial parthenogenesis, he says:

> It seems that the essential feature of the process of fertilization consists first in a liquefaction or hydrolysis or both, of fatty compounds, and second, in the starting of processes of oxidation in the right direction. These processes of liquefaction of fats and hydrolysis and oxidation form apparently the basis of the synthesis of nucleins. It is possible, but far from proved, that among the fatty compounds involved in the process of hydrolysis are the lecithins.
>
> These results are in harmony with the facts observed in the germination of oily seeds. The process of germination is an analogue to the starting of the development in the animal egg, inasmuch as resting cells are thrown into the process of cell division and this process is based upon the synthesis of nucleins. . . . . I think the chemistry of the germination of seeds is essentially the chemistry of nuclein synthesis, and I believe the method of starting this synthesis is essentially the same as in the fertilization of the egg. . . . . I am of the opinion that this mechanism of nuclein synthesis is the thread by which we can find a rational way through the maze of the otherwise bewildering mechanisms, characteristic of living matter; on one hand, the phenomena of growth, on the other, those of self-preservation. . . . . We must therefore conclude that the nuclei themselves or one of their constituents are the catalyzer for the nuclein synthesis or one phase of it. It is possible that the nucleus catalyzes only the phenomena of oxidation, and inasmuch as oxidations are the *conditio sine qua non* of nuclein synthesis, this would explain the autocatalytic effect of the nuclei upon this reaction.

It will be difficult to harmonize with this theory the germination of rice seed which, according to TAKAHASHI, germinate in the absence of oxygen, and the anaerobic growth of young shoots, described by NABOKICH.—C. R. B.

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[15] Science N. S. **26**:425–437. 1907.

Leaf structure and physical factors.—Most American ecologists have paid attention to the distributional rather than to the anatomical phases of their subject. For this reason the contribution of Mrs. CLEMENTS[16] has been particularly welcome. Few if any investigators have so thoroughly related leaf structure to definite physical factors. After a brief historical sketch, and a survey of the physical factors studied (light, water content of the soil, humidity, temperature), a detailed presentation is given of the characteristics of the mesophyll and epidermis of a large number of the plant species of various habitats in the Pike's Peak region of Colorado. The plants are divided into two classes, those confined to one habitat, and those that occur in two or more habitats (polydemic species). The latter seem to be the most numerous, and of course are the most interesting, as showing the range of specific variation. The various types of polydemic species are grouped so as to bring out graphically the effects of the various factors. The use of the word endemic for plants confined to one habitat, and mesophyll for a mesophytic leaf seem unfortunate in view of the long and wide use of these words in other senses. Among the more interesting of the results and conclusions, we may note that the lack of palisade cells is regarded as adaptational in many hydrophytes, but hereditary rather than adaptational in monocotyls; a typical xerophyte is regarded as having the chlorenchyma made up entirely of palisade cells; while light is regarded as the dominant factor in determining the palisade structure and close cell texture in xerophytes, dryness of air or soil is necessary for the extreme expression of this result. This paper is one that should stimulate many to carry on work along the lines of ecological anatomy.—HENRY C. COWLES.

Tomato rot.—The blossom end rot of tomatoes is again the subject of study. This is a widespread disease which has been studied repeatedly but without concordant results. The rot has been heretofore variously attributed to Macrosporium, Fusarium, Cladosporium, and to bacteria, while some workers have failed to find any parasites at all. The latest bulletin, by Miss SMITH,[17] describes the discovery, after very careful search, of small tufts of a colorless mycelium, protruding from intercellular spaces between the blackened walls into the still healthy tissue. Affected pieces of tissue in a moist chamber repeatedly developed an abundant growth of Fusarium. The affected tissue showed no bacteria. Pure cultures of the Fusarium were isolated and inoculations upon green fruit were successful, sometimes through the style but much more frequently through punctures in the epidermis. This disease does not develop well or at all upon old tomatoes, its damage being limited to young fruit. The writer correlates this fact with the increase of malic acid as the fruit increases in size; since her cultures prove that malic acid is extremely unfavorable to the growth of this species of Fusarium.

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[16] CLEMENTS, EDITH S., The relation of leaf structure to physical factors. Trans. Amer. Mic. Soc. **1905**:19–102.

[17] SMITH, ELIZABETH H., Mass. Agr. Exp. Sta. Technical Bull. 3. April 1907.

A bacterial rot of the tomato is also described in this bulletin. The bacteria were isolated from tomatoes which showed no sign of fungus growth. They were cultivated in pure culture and when reinoculated into the tomato fifty out of a total of sixty-seven inoculations produced the characteristic disease. There are thus two distinct diseases: a rot due to Fusarium and another rot due to bacteria.—F. L. STEVENS.

Root tubers of Dioscorea.—Some years ago QUÉVA described the vegetative organs of certain species of Dioscorea, and reached the conclusion that the tuberous body which occurs at the end of some of the roots represents an organ which has changed its nature from root to "something else." The matter was taken up by GOEBEL, who explains this peculiar body as an organ whose morphology lies between a shoot and a root. A much more simple and more natural explanation has recently been offered by LINDINGER,[18] who has studied *D. discolor*, and concludes that the roots do not change their morphological nature, but their function. The root consists of a slender, cylindric, basal portion, and a tuberous apical one, the former functioning as a nutritive, the latter as a storage root, which is also able to produce root-shoots. The anatomical structure of both regions is discussed, and it is interesting to notice that in the tuberous part the mestome strands are not arranged in a circle; that the inner mestome strands are collateral; and that, at least in some portions of the tuber, no endodermis is differentiated.—THEO. HOLM.

Secretory organs of Menispermaceae.—According to MAHEN,[19] these consist of ducts with tannin, ducts with caoutchouc, and secretory cells. Ducts with tannin occur in the cortex and pith of the stem, in the primary cortex of the root, in the parenchyma of the petiole, and in the midrib of the leaf. They are tubes of considerable length, and very often difficult to detect without tests for tannin; and are characteristic of certain species of Anamirta, Cocculus, Cissampelos, Burasaia, Calicocarpum, etc. Ducts with caoutchouc are known only in Tinomiscium, being found in all the vegetative organs as follows: in the stem, around the sclerenchymatic arches of the pericycle and in the pith; in the leaf, in midrib and petiole around the mestome strands. They are tubular and very thin walled. The latex is white and granulose, readily soluble in chloroform, but only partly so in absolute alcohol and ether. The secretory cells, observed only in *Abuta rufescens*, and containing an essence, abound in the stem near the sclerenchymatic pericyle on its outer and inner face.—THEO. HOLM.

A Linnean herbarium.—Although the herbarium of LINNAEUS went to London after his death, several other collections made by him and his pupils remained in Sweden, but have not been accessible until recently. In fact, it was not known where they were until the newly appointed curator of botany at the Swedish Academy, Professor C. A. M. LINDMAN,[20] discovered them among other bundles of plants stored away in "lumber rooms." These collections consist of the herbaria of CARL VON LINNÉ fil., ALSTROEMER, MONTIN, and SOLANDER, and contain many specimens named by LINNAEUS himself. These plants of LINNAEUS and his son, and from *Hortus Upsaliensis* during the lifetime of LINNAEUS, aggregate about 2000. They have been brought together as a "Herbarium Linnaeanum," and LINDMAN is now publishing a list of the species, arranged according to *Syst. Veget.* ed. 13 (1774) and *Suppl. Plant.* (1781).—THEO. HOLM.

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[18] LINDINGER, LEONHARD, Ueber den morphologischen Wert der an Wurzeln enstehenden Knollen einiger Dioscorea-Arten. Beih. Bot. Centralbl. **21**:311. 1907.

[19] MAHEN, JACQUES, Sur les organes sécréteurs des Menispermacées. Bull. Soc. Bot. France **53**:651. 1906.

Climate and plants.—H. VON GUTTENBERG[21] has made an anatomical and physiological study of the evergreen element of the Mediterranean flora, in part quite parallel to the studies which BERGEN has published in this journal and to some extent upon the same species. His work, however, was more extensive. It was done upon two islands, Lussin and Brioni Grande, near the Austrian coast of the Adriatic, and while his results as to transpiration do not always agree with BERGEN'S, their general drift is the same. The anatomical structure of the leaves is not of the extreme xerophilous type, because these plants must be able to take advantage of the more favorable conditions of spring and autumn, as well as to withstand the drought of summer. Thus, he finds the guard cells characterized by a special motility because of the "hinge" in the wall, so that they can prevent transpiration almost entirely by complete closure or allow it freely by wide opening. We may pe permitted some skepticism as to the perfection of this regulation, however.—C. R. B.

Anatomy of lianes.—FRIES[22] describes the anatomy of the stem and the aerial roots of a cucurbit, *Siolmatra brasiliensis*, with some notes on the mode of origin and form of the aerial roots of a species of Cissus, both occurring in the rain-forests of northern Argentina and southern Bolivia. Only two cases of the formation of aerial roots have been described among Cucurbitaceae, and in these the roots are small and known only in house-grown plants. But Siolmatra produces the long rope-like roots, reaching down from the tops of the highest trees, where the plant expands its foliage, to enter the ground and branch profusely. The most remarkable anatomical character of the stem is the presence of a secondary cambium in the pith, which produces groups of leptome and mechanical tissues on its inner face and groups of libriform cells on its outer face.—C. R. B.

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[20] LINDMAN, C. A.M., A Linnaean herbarium in the Natural History Museum in Stockholm. Arkiv. för Botanik Roy. Swed. Acad. Stockholm **7**:no. 3. 1907.

[21] GUTTENBERG, H. VON, Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Engler's Bot. Jahrb. **38**:383–444. *pls. 7–9.* 1907.

[22] FRIES, ROB. E., Morphologisch-anatomische Notizen über zwei südamerikanische Lianen. Bot. Studier tillägnade F. R. KJELLMAN 89–101. Upsala. 1906.

Driftwood from the arctic sea.—A large amount of driftwood has been examined by Ingvarson,[23] from Spitzbergen, Beeren Island, Jan Mayen, Greenland, and the mouth of Jenisei River. Among the conifers are species of Larix, Picea, Pinus, and Abies; while the deciduous plants belong mostly to Salix, Populus, and Betula. The structure of the trunks and roots is described and figured. The author reaches the conclusion that the polar current is a much more important factor in the transportation of driftwood in the arctic seas than is the gulf stream. The fact that seeds and fruits of various arctic plants have been found caught in the fissures of driftwood leads to the conclusion that the wide distribution of several arctic species may be due to such transportation.—Theo. Holm.

A mutant of Leptospermum scoparium.—This shrub is very common in New Zealand, occupying vast tracts of usually barren country. The flowers are white, and the close-growing shrubs when in full bloom look as if densely powdered with snow. Pink forms are found now and then, but Cockayne[24] records the sudden appearance of a single plant with rich crimson flowers. This plant was taken possession of by a firm of nurserymen, and among the progeny obtained from the seed six more plants with crimson flowers appeared. The variation extends also to the size and color of the leaves, which are brownish instead of green.—J. M. C.

Linnaea borealis.—Wittrock[25] has published thirteen mostly colored plates of Swedish forms of this species, and in the accompanying text has described about 160 forms. The vegetative organs are mentioned, but the author has made a special study of the shape and coloration of the corolla, which is beautifully illustrated. The American representatives are briefly described, and the following may be noted: *L. borealis longiflora* Torr. f. *angustissima* (Washington), f. *curticalyx* (Colorado), f. *minutifolia* (Vermont), f. *integerrima* (Alberta).—Theo. Holm.

Monograph of Fraxinus.—Lingelsheim[26] has made a general study of Fraxinus as to its morphology (in the old sense), anatomy, geographical distribution, fossil forms, phylogeny, and classification. He recognizes twenty-seven species in § Ornus, nine of which are new; and thirty-two species in § Fraxinaster, four of which are new. The four new Fraxinasters are *F. rufescens* (Jaral 1315), *F. papillosa* (Townsend & Barber 354), *F. Pringlei* (Pringle 9417), all from Mexico, and *F. hybrida* from Florida (Curtiss 2321, Nash 941 and 1698).—J. M. C.

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[23] Invgarson, Fr., Om Drifverden i Norra Ishafvet. Köngl. Svenska Vet. Akad. Hdlgr. **37**:1. 1903.

[24] Cockayne, L., On the sudden appearance of a new character in an individual of *Leptospermum scoparium*. New Phytol. **6**:43–46. 1907.

[25] Wittrock, V. Br., *Linnaea borealis* L., species polymorpha et polychroma. Acta. Hort. **4**:no. 7. 1907.

[26] Lingelsheim, Alexander, Vorarbeiten zu einer Monographie der Gattung Fraxinus. Bot. Jahrb. **46**:185–223. *pl. 8.* 1907.

Flora Boreali-Americana.—It is generally conceded that ANDRÉ MICHAUX was not the real author of this work, and that it should be credited to RICHARD. CLOS[27] has brought the subject up again, and we learn that KUNTH in 1825 declared positively that RICHARD was the anonymous author of the work; and that RICHARD published very little himself, leaving to his friends and pupils the publication of many of his most important contributions. BEAUCHARDAT made a similar declaration before the faculty of medicine in Paris, in 1853.—THEO. HOLM.

Origin of asparagin in seedlings.—SCHULZE[28] has contemplated the work of others in connection with some of his own and offers in consequence the view that by the oxidation of the primary products of the dissociation of proteid (mono-amino-acids, hexone bases) ammonia is formed, and that the ammonia is then used in metabolism for the synthesis of asparagin and glutamin as the case may be. That enzymes are potent in the oxidation of the primary products mentioned he regards as probable.—RAYMOND H. POND.

Photosynthesis.—An excellent but all too brief résumé of the recent progress and present status of the problems of photosynthesis and the rôle of chlorophyll, given by KOHL[29] before the general meeting of the German Botanical Society in June 1906, has only recently been published in the *Berichte* (May 1907). It was too early to take account of the latest work of USHER and PRIESTLEY,[30] which would have modified radically some of its statements.—C. R. B.

Myxomycetes of Colorado.—BETHEL and STURGIS have begun the publication of a series of contributions under the general title "The Myxomycetes and Fungi of Colorado," the first number being a presentation of the Myxomycetes by STURGIS.[31] This first bringing together of the slime moulds of the state shows almost 100 species, representing 28 genera.—J. M. C.

Chromosomes of Oenothera mutants.—Miss LUTZ[32] has counted the chromosomes in the root tips of seedlings of *O. Lamarckiana* and of *O. gigas*, one of its mutants. The point of chief interest is that the number (probably 28) in the somatic cells of this mutant is double that found in the parental form.—J. M. C.

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[27] CLOS, D., La première flore de l'Amérique du Nord et Louis Claude Richard. Bull. Soc. Bot. France 53:667. 1906.

[28] SCHULZE, E., Zur Frage der Bildungsweise des Asparagins und des Glutamins in den Keimpflanzen. Ber. Deutsch. Bot. Gesells. 25:213–216. 1907.

[29] KOHL, F. G., Kohlensäure-Assimilation und Chlorophyll-Funktion. Ber. Deutsch. Bot. Gesells. 24:(39)–(54). 1907.

[30] See BOT. GAZETTE 43:144. 1907.

[31] STURGIS, W. C., The Myxomycetes of Colorado. Colorado Coll. Publ., Sci Series 12:1–43. 1907.

[32] LUTZ, ANNE M., A preliminary note on the chromosomes of *Oenothera Lamarckiana* and one of its mutants, *O. gigas*. Science N. S. 26:151, 152. 1907.

Structure of chloroplasts.—The examination of living and fixed chloroplasts of Chlorophytum and Selaginella convinces PRIESTLY and IRVING[33] that the chlorophyll occupies the peripheral layer, 1–3 μ thick, where it is held in the meshes of a network. The observations of TIMIRIAZEFF and NÄGELI on the splitting of the chloroplast when placed in a solution of low osmotic pressure are confirmed.—C. R. B.

Zymase from Aspergillus.—JUNITZKY[34] finds that the aerobically cultivated mycelium of Aspergillus always contains some zymase. He regards this result as favoring rather than as opposing the theory of the genetic connection of alcohol-fermentation with aerobic respiration.—RAYMOND H. POND.

Carex in N. W. America.—HOLM[35] has published an account of the genus Carex in northwestern America, the topics being (1) a synopsis of the species, (2) types characteristic of northwest America, and (3) the geographical distribution of the Carices of northwest America.—J. M. C.

Rate and period of growth of Polyporus.—EDGERTON[36] has found that the growth of *Polyporus lucidus* is exogenous and averages about 0.5^{cm} a day for the growing-period; and that the change in the development from stalk to pileus is a gradual process.—J. M. C.

Julianaceae.—The full paper dealing with this interesting new family of Mexican plants has now appeared.[37] The preliminary abstract for presentation before the Royal Society was noticed in this journal.[38]—J. M. C.

Aerenchyma.—WITTE[39] describes and figures the aerenchyma in *Lysimachia vulgaris* produced in stems in water, and records the production of this tissue in seven species of the Swedish flora.—C. R. B.

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[33] PRIESTLY, J. H., and IRVING, ANNIE A. The structure of the chloroplast considered in relation to its function. Annals of Botany **21**:407–413. *figs. 2.* 1907.

[34] JUNITZKY, N., Ueber Zymase aus *Aspergillus niger.* Ber. Deutsch. Bot. Gesells. **25**:210–212. 1907.

[35] HOLM, THEO., The genus Carex in northwest America. Beih. Bot. Centralbl. **22**^{2}:1–29. 1907.

[36] EDGERTON, C. W., The rate and period of growth of *Polyporus lucidus.* Torreya **7**:89–97. 1907.

[37] HEMSLEY, W. BOTTING, On the Julianaceae: a new natural order of plants. Phil. Trans. Roy. Soc. London B **199**:169–197. *pls. 18–24. figs. 23.* 1907.

[38] BOT. GAZETTE **42**:236. 1906.

[39] WITTE, HERNFRID, Ueber das Vorkommen eines aërenchymatischen Gewebes bei *Lysimachia vulgaris* L. Bot. Studier tillägnade F. J. KJELLMAN 265–274. *figs. 10.* Upsala. 1906.

NEWS

Mr. W. Eric Brooks has succeeded Mr. V. H. Blackman in the department of botany of the British Museum.

Mr. A. W. Hill, lecturer at Cambridge University, has been appointed assistant director of the Royal Gardens, Kew.

Edward W. Berry spent the summer in collecting Mesozoic and Pleistocene fossil plants in Virginia and North and South Carolina.

Mr. T. D. Beckwith, Department of Agriculture, has been elected assistant professor of bacteriology and plant pathology at the North Dakota Agricultural College and Experiment Station, Fargo, N. D.

Mr. J. H. Schaffner, professor of botany at Ohio State University, has been granted leave of absence of one year to study in Germany. His work at the university will be cared for by Dr. A. Dachnowski, University of Michigan.

A biographical sketch of the late Maxwell T. Masters is published in Kew Bull. Misc. Inf. **1907**:325–334, prepared by Mr. W. B. Hemsley. A bibliography is also published, not including contributions to the *Gardeners' Chronicle*, and containing 141 titles.

Dr. Th. Herzog, of Freiburg, has gone to South America for a stay of eighteen months, having been appointed botanist of a Portuguese commercial society organized to introduce "plant products" into Europe. His explorations will lie chiefly in Bolivia and the Amazon region, and in connection with his other work he hopes to obtain valuable collections of plants, and especially of mosses.

Mr. C. F. Baker, for three years past chief of the Department of Botany in the Estación Central Agronomica, at Santiago de las Vegas, Cuba, has been appointed curator of the Herbarium and Botanic Garden at the Museu Goeldi Pará, Brazil. All letters and packages should be addressed to him at that point after November 1, 1907. His especial function there will be the further development of the herbarium and garden at Pará, and the botanical exploration o some of the most interesting parts of the Amazon Valley.

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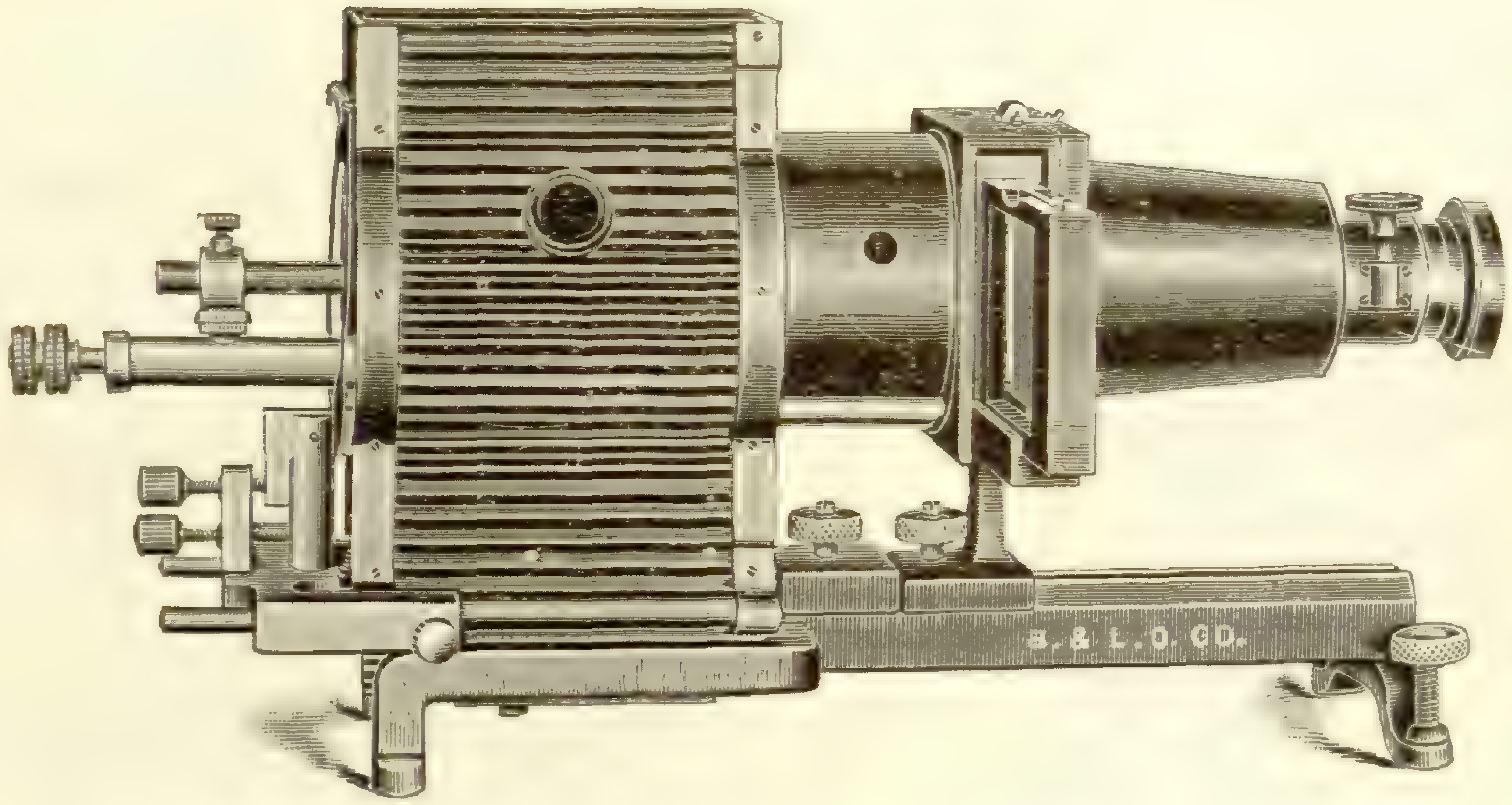

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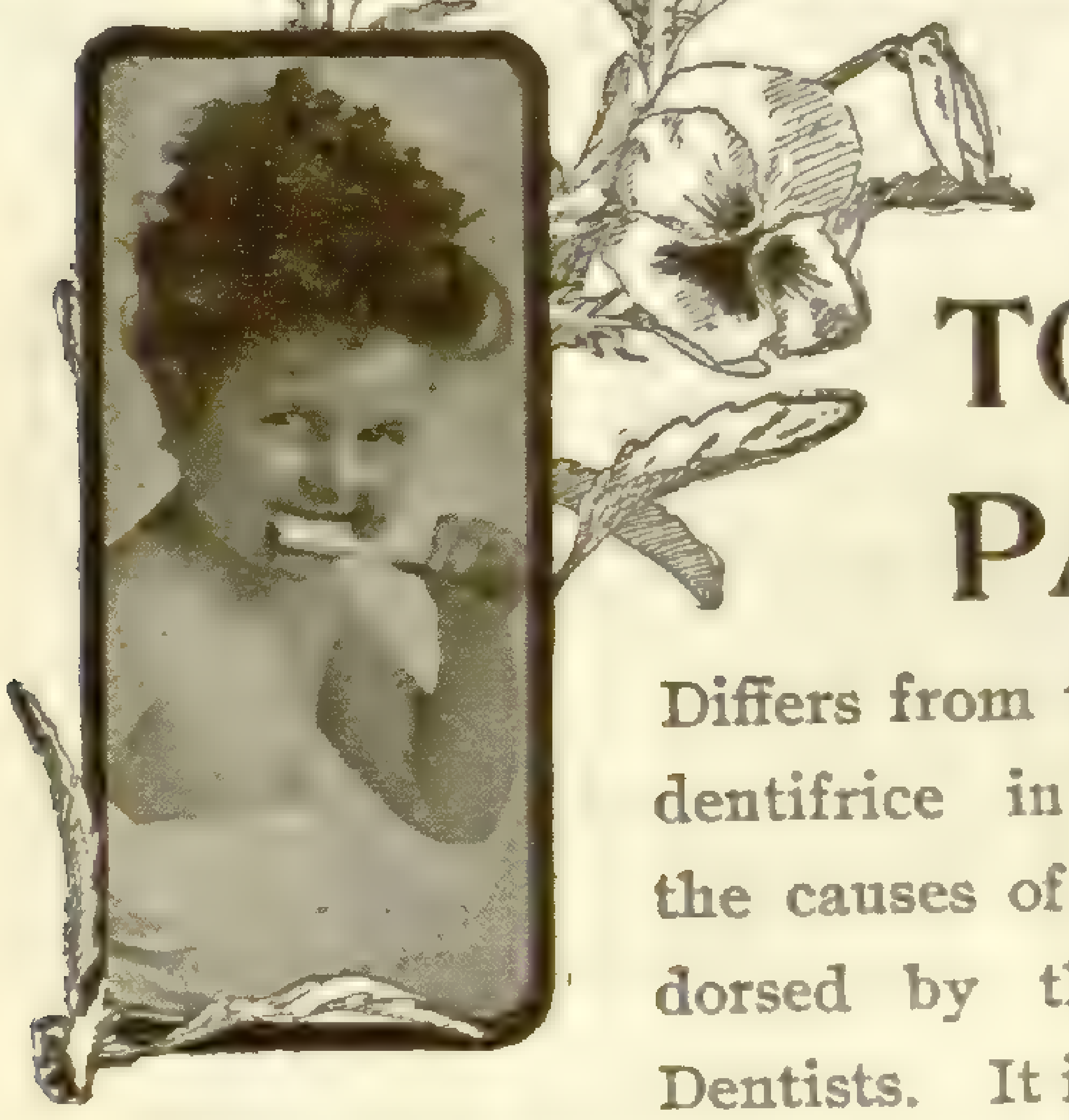

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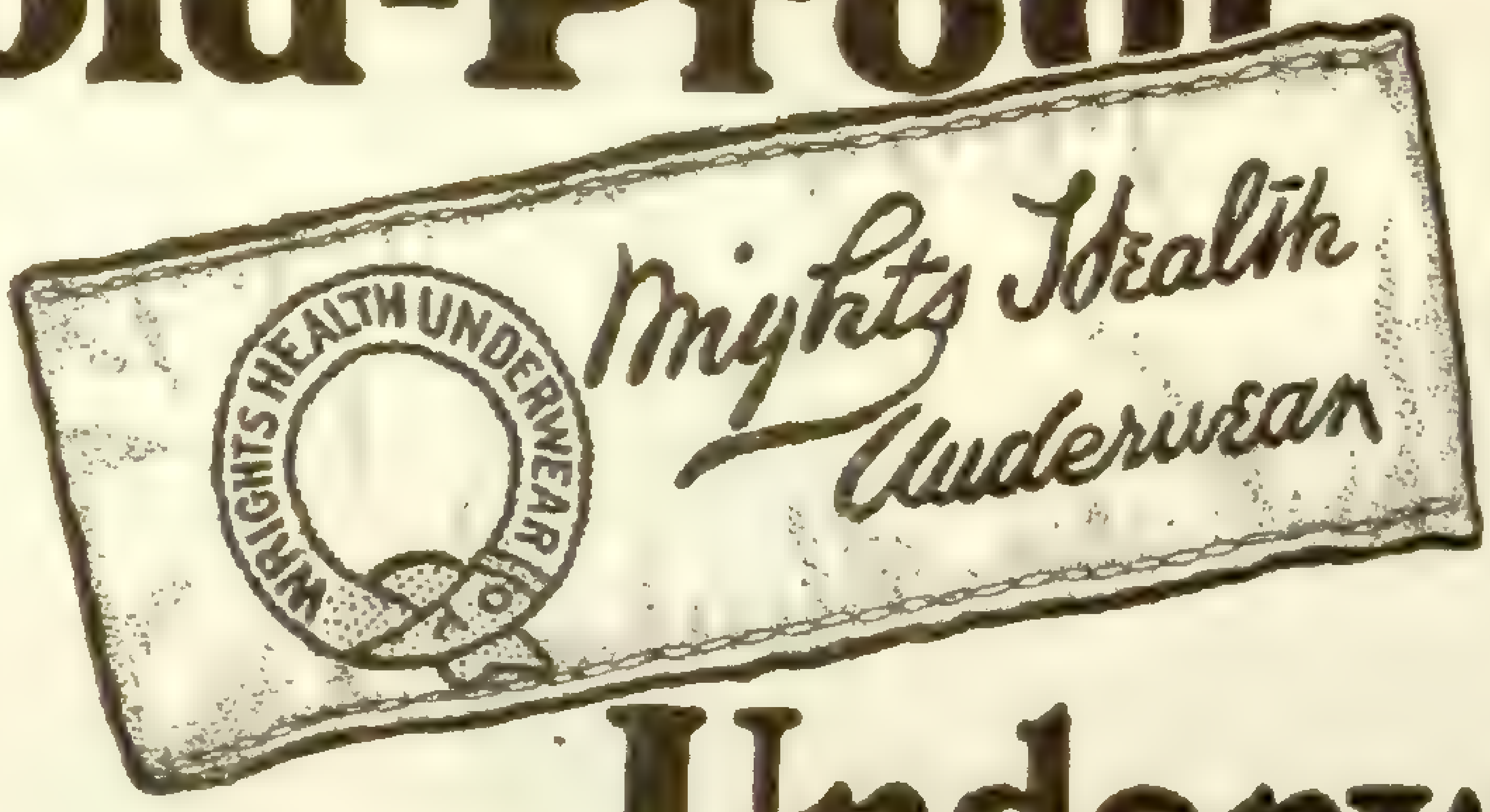

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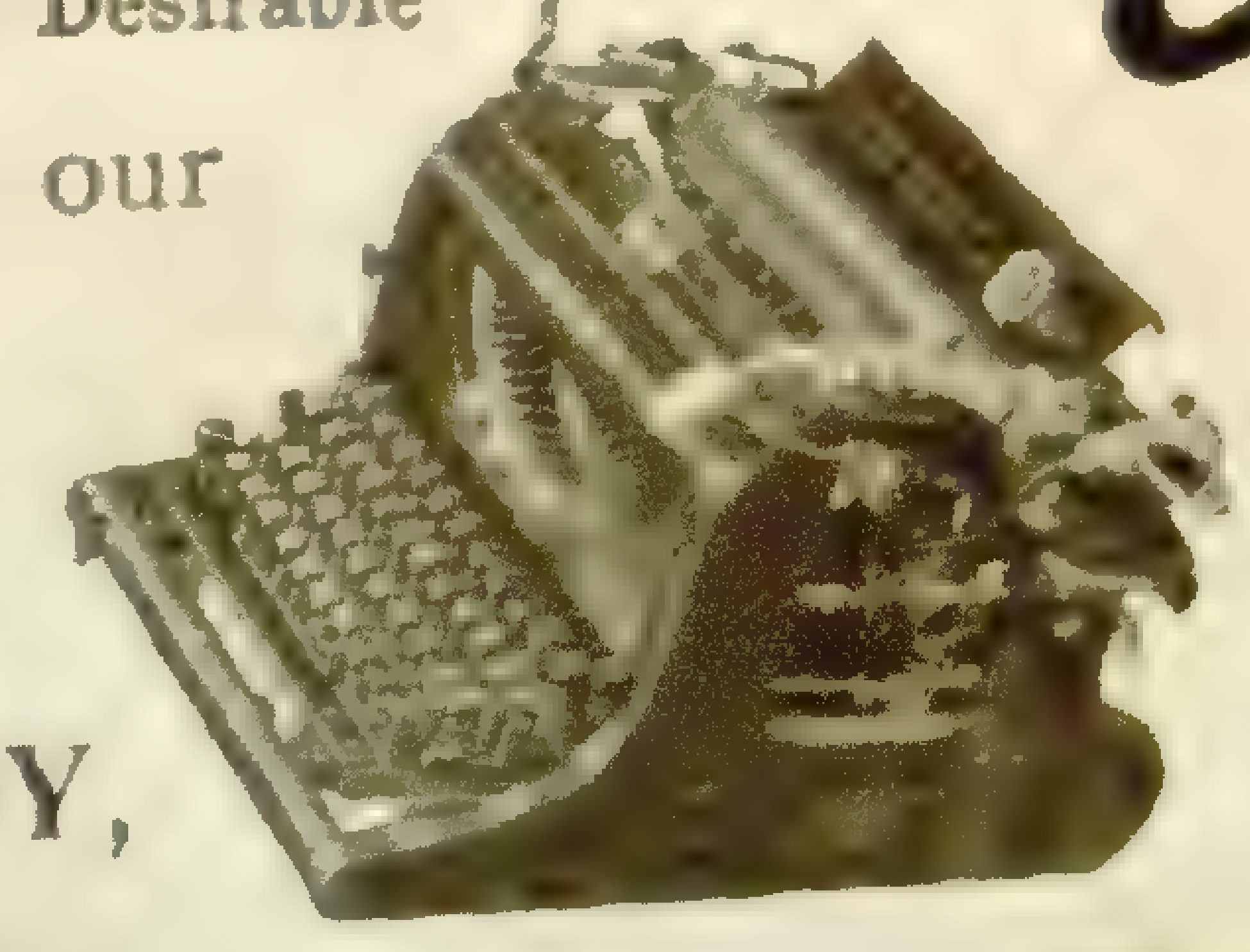

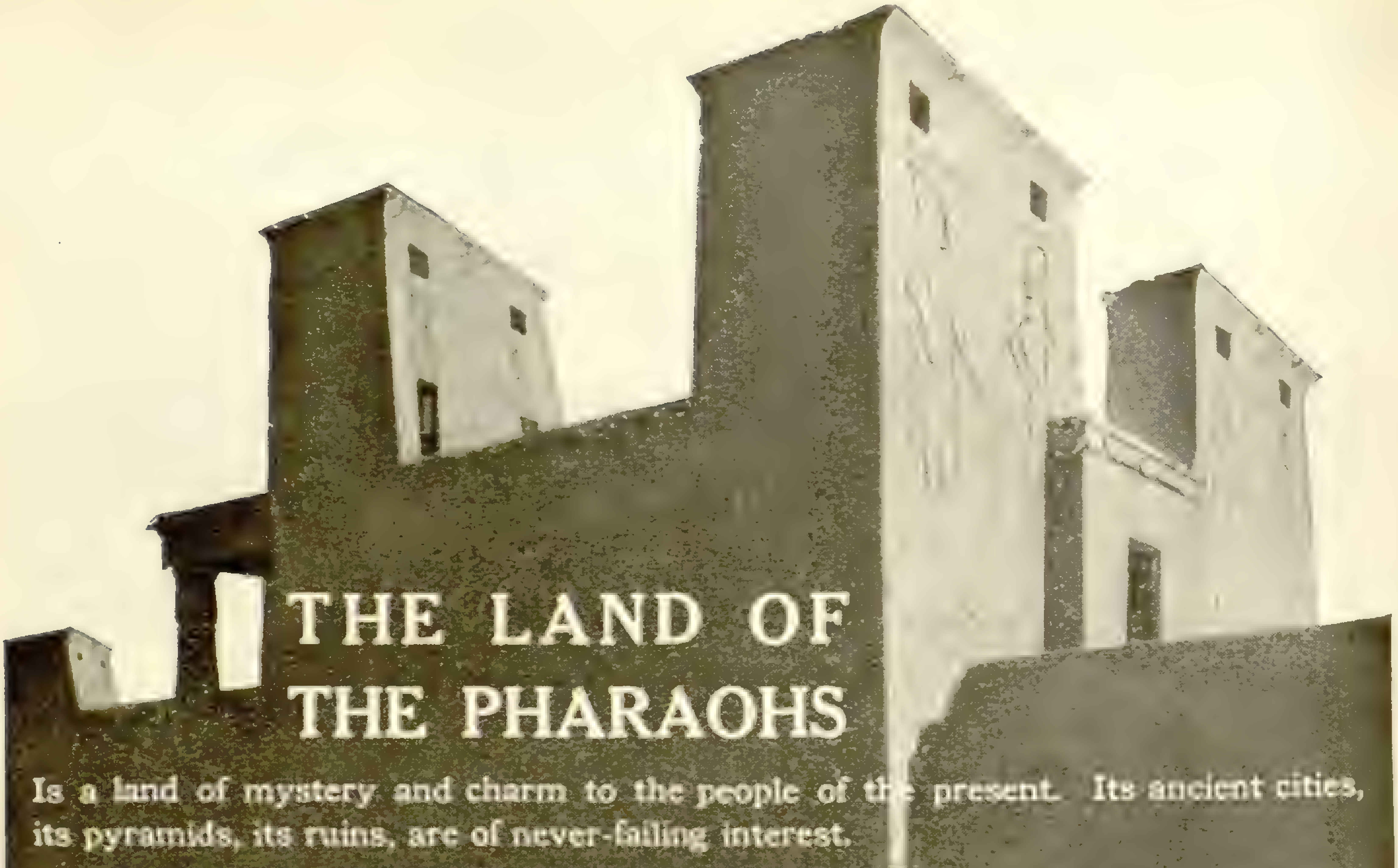

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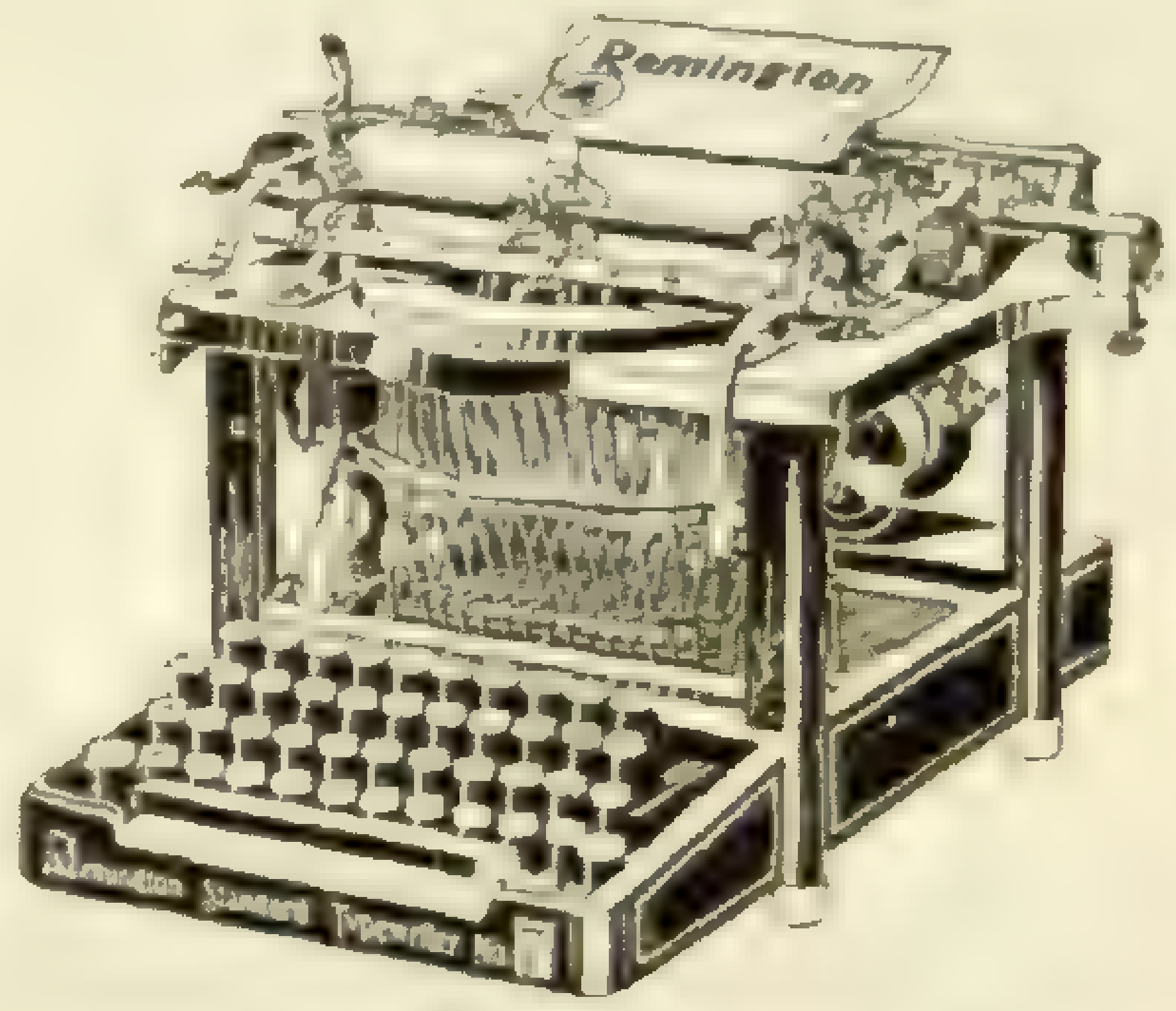

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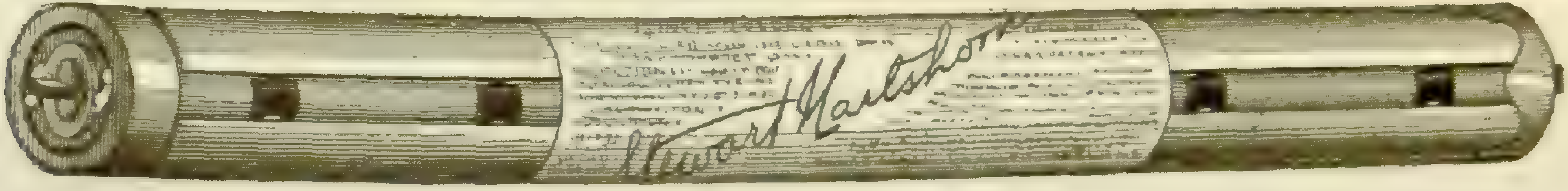

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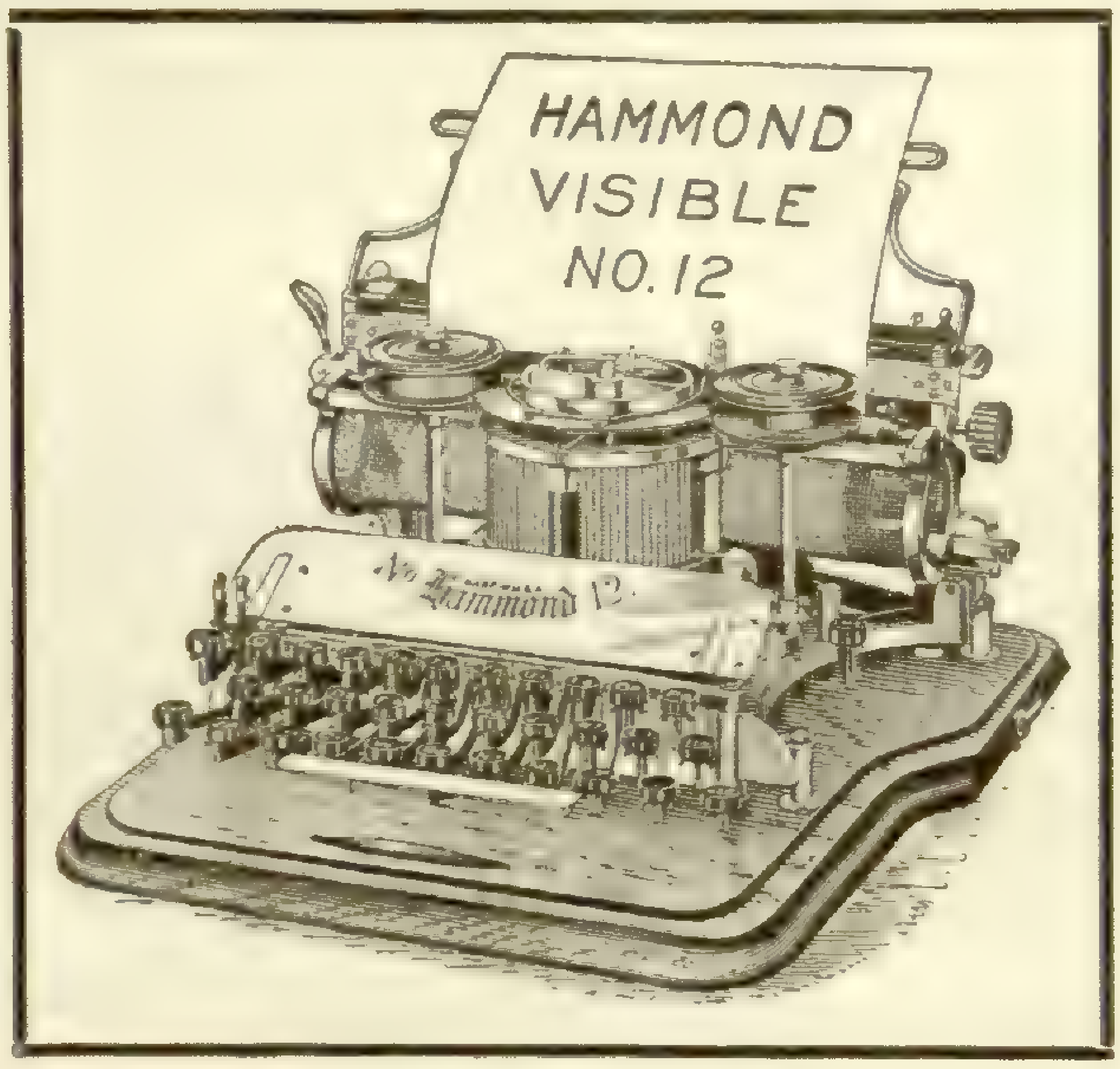

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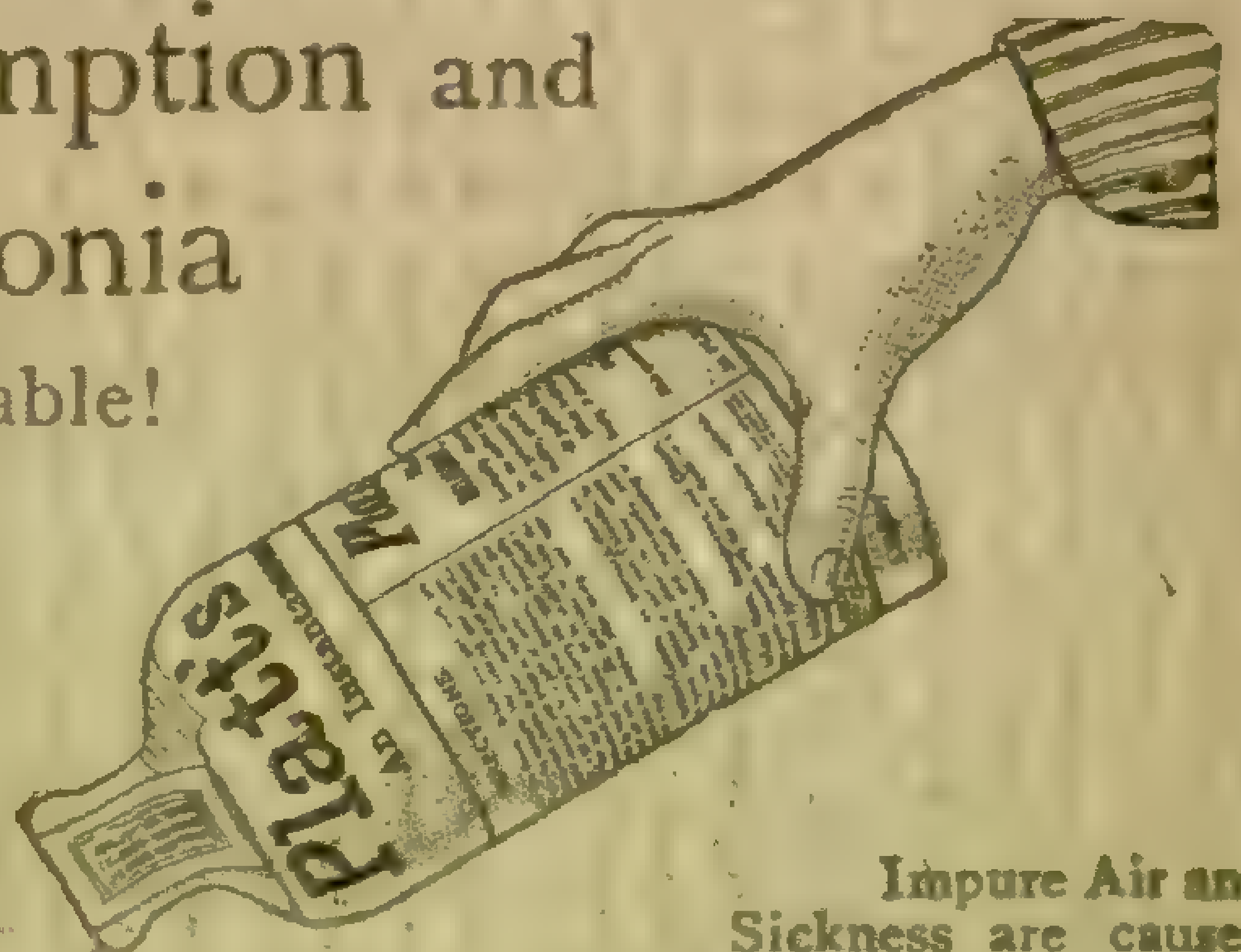

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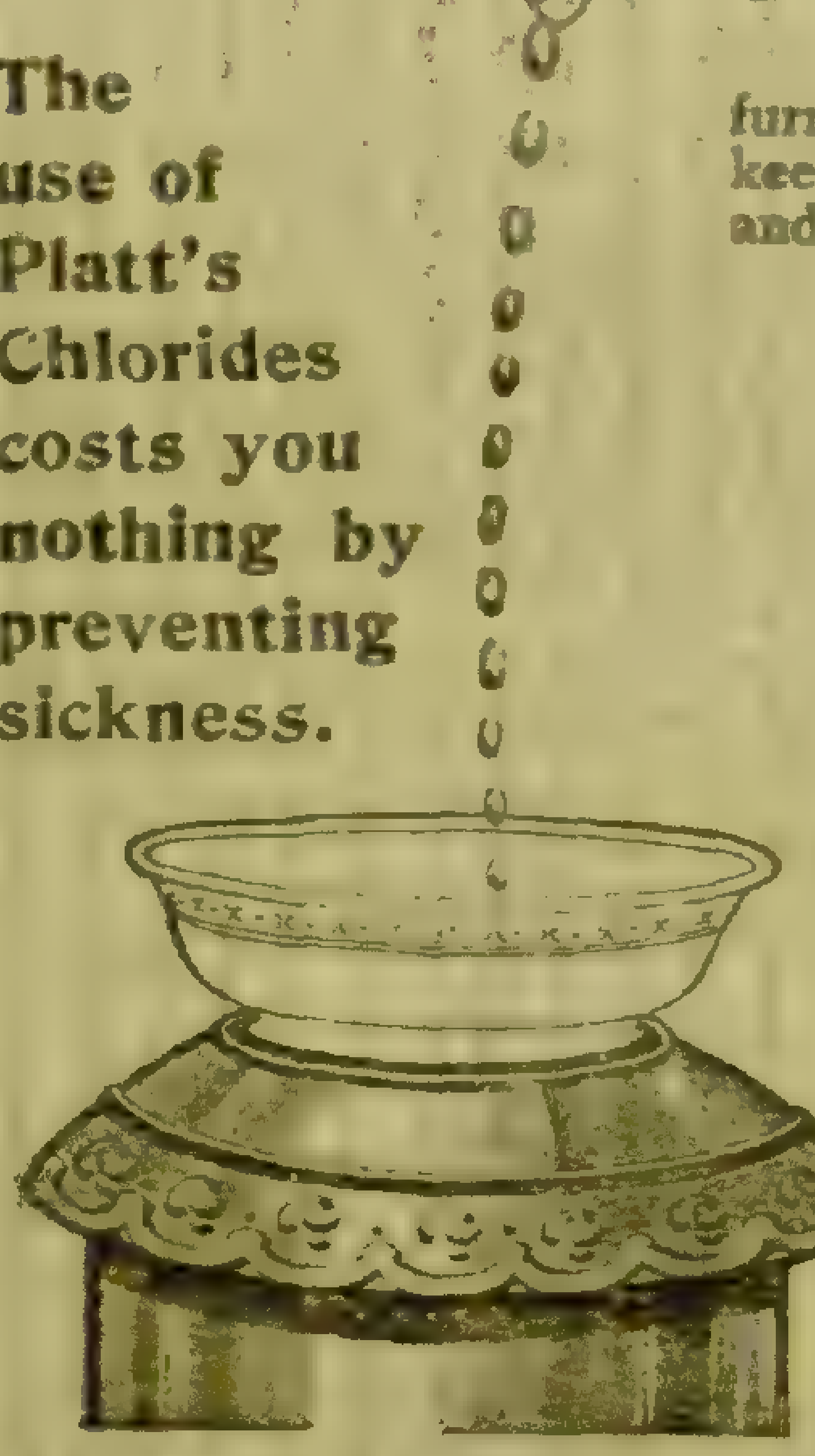

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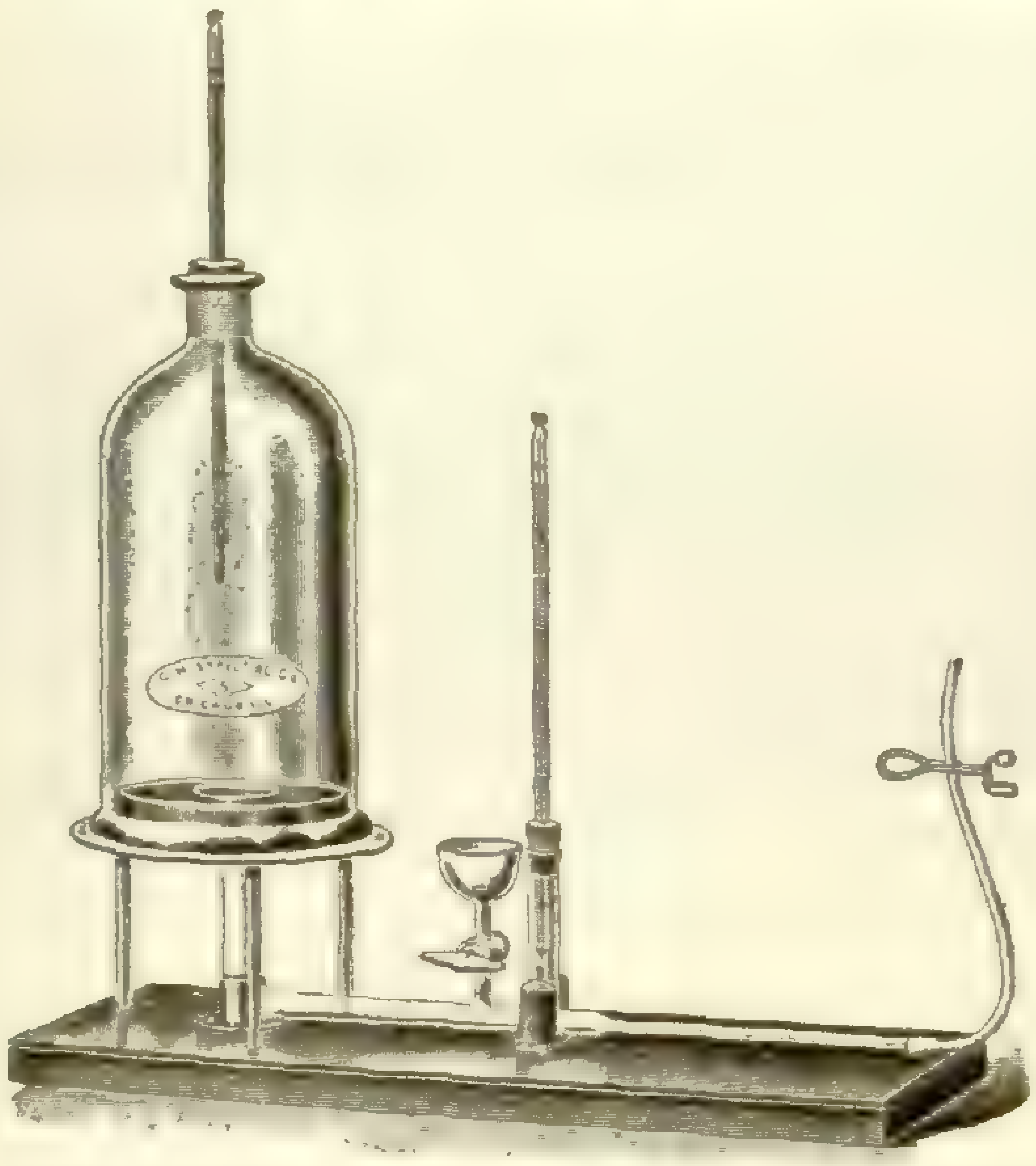

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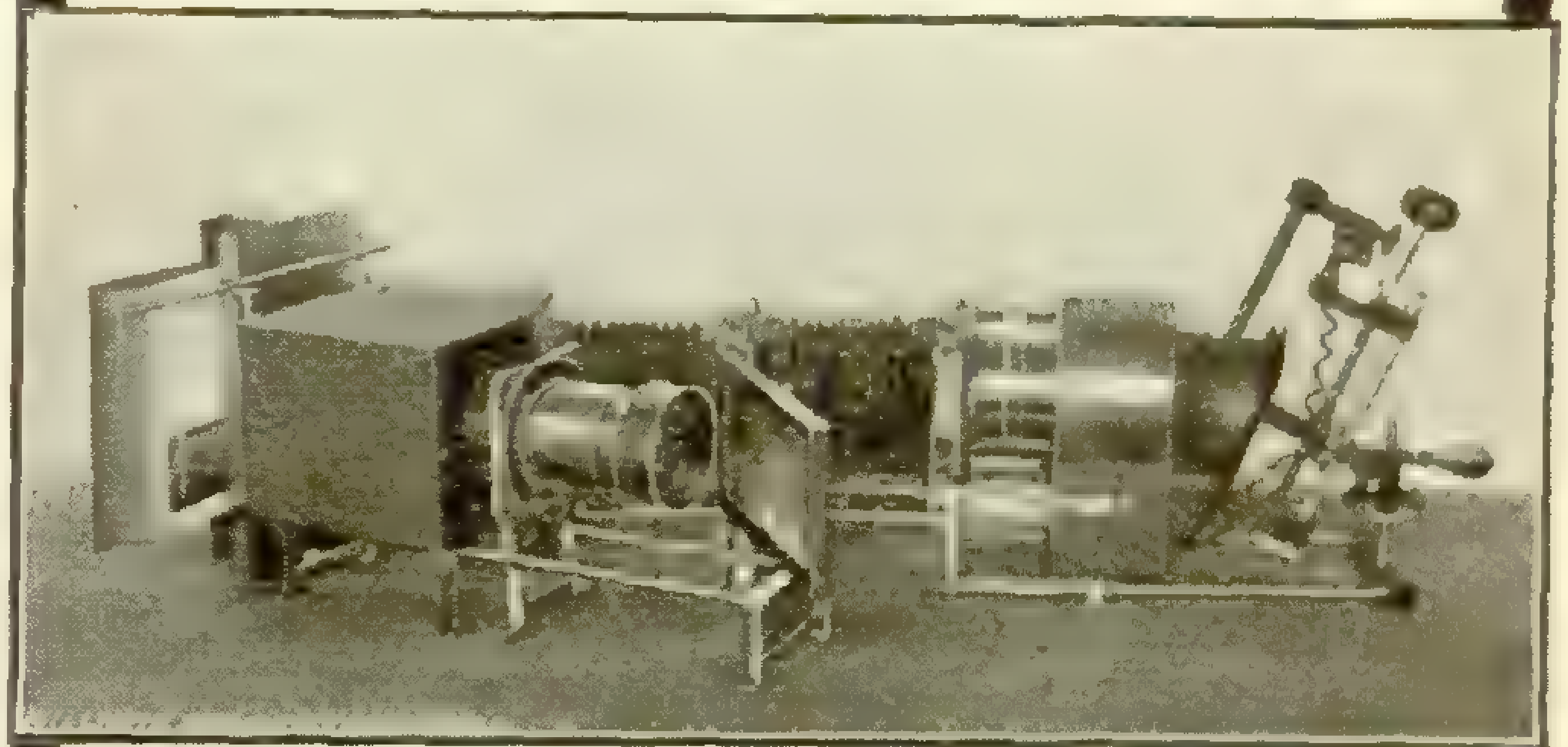

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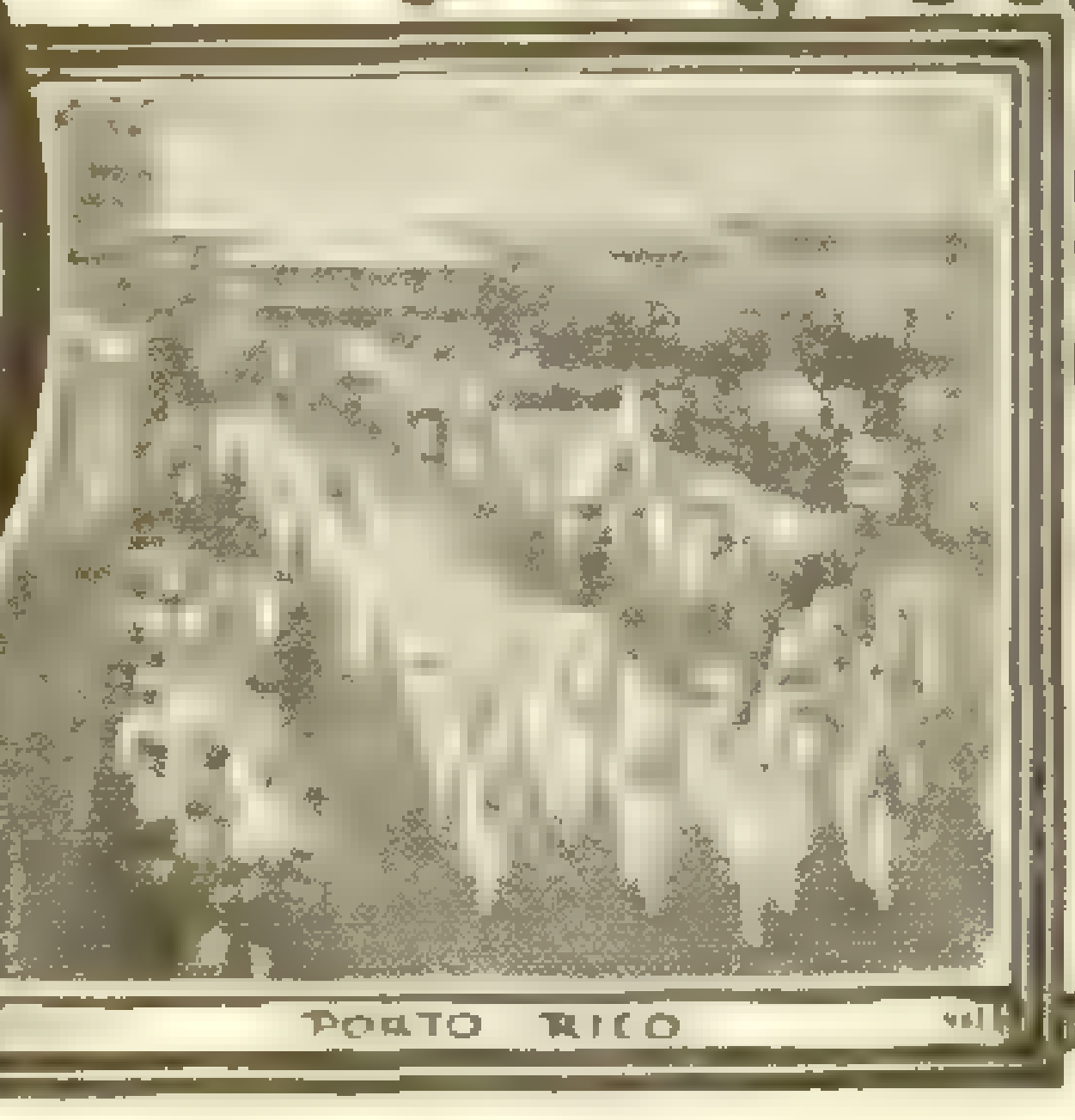

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HUGO DE VRIES

In the group Onagra of the evening primroses the hybrids between different species are, as a rule, constant and uniform through the succeeding generations. In this respect they comply with the common rule for the majority of the characters of specific hybrids. Only, on account of the scarcity of regressive marks in this group, the phenomenon of constancy is allowed to show itself pure and complete. An exception is afforded by *Oenothera brevistylis*, the character of which splits up according to the formulae of MENDEL.[1]

As an example of a constant hybrid race I quote the *O. muricata* × *biennis*. It has been found uniform through at least four generations. In the second, the one in which Mendelian marks are seen to split, I cultivated over 80 flowering plants and over 100 rosettes, but no differences could be detected. Last summer (1907) I cultivated, on neighboring beds, 35 plants of the first and 18 of the fourth generation. Both groups produced a number of flowering stems, but, apart from the ordinary fluctuating variability, the characters were exactly the same in all the specimens. They had the flowers almost like those of *O. biennis*, but dense and richly flowered spikes like the *O. muricata*.

The types of the species used for this experiment were the forms which occur everywhere on waste places throughout Europe, having been introduced, the first from Virginia and the second from Canada, about three centuries and one century ago respectively. They are probably the types on which LINNAEUS based his descriptions of the species. In the United States, however, these Linnean species consist of quite a number of subspecies, of which I collected over a dozen in Kansas, Missouri, Illinois, and elsewhere, during the summer of 1904. On sowing them in my experiment garden, I observed them to be fairly distinct, each constituting a sharply defined type. The form which is the most common throughout the United States is not the same as the one introduced into Europe, neither for *O. biennis* nor for *O. muricata,* as has also been pointed out by MACDOUGAL for *O. biennis.*

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[1] Die Mutationstheorie 2:429.

All these numerous elementary species agree with one another in a most interesting character. Their anthers touch the stigma, open themselves in the bud, and produce fertilization before the flower opens. The process is almost entirely finished before the insects are admitted. Crosses seem to be very rare in nature, although they do occur, since I collected the hybrid of *O. muricata* and *O. biennis* in the dunes near Amsterdam, and even more than once. A simple means of pure self-fertilization may be derived from this pollination within the bud. I cut the buds of our *O. biennis* one or two hours before opening, cutting through the middle of the tube, and the pods developed as strongly and produced as many good seeds as those whose flowers were allowed to be visited by bees. The flowers of *O. Lamarckiana, O. Hookeri,* and other large-flowered species, on the contrary, are not fertilized in the buds, but are in need of the help of insects (moths, bees, and bumble-bees).

The specific hybrids of this group of Onagra differ in a very conspicuous way from ordinary hybrids in so far as the reciprocal forms often are not identical, but differ widely from one another.[2] Although I have observed this fact in numerous cases, it is not a general rule. The hybrid *O. Lamarckiana*×*gigas* is identical with *O. gigas*× *Lamarckiana.* In the same way the species of the subgenus Euoenothera crossed with those of Onagra yield uniform hybrids. I crossed the *O. Sellowii* with *O. biennis, O. muricata,* and *O. Lamarckiana* and observed their reciprocal hybrids to be identical.

Within the group of the Onagras, however, the reciprocal hybrids are in most cases different, and with a few exceptions are more similar to their father than to their mother. They are, as it is called, patroclinous. So it is, for instance, with the reciprocal hybrids of *O. muri-*

[2] Die Mutationstheorie 2:471.

cata and *O. biennis* in their subspecies from our European dunes. The *O. muricata*×*biennis* looks like *O. biennis* and might be mistaken for it, since it is broad-leaved and large-flowered. The *O. biennis*×*muricata*, on the other hand, is narrow-leaved and small-flowered like its male parent. During the summer of 1907 I cultivated the first and second generations of the latter type and found them uniform, but in almost all respects different from the *O. muricata*×*biennis*. Especially the flowers are of a deep yellow and strongly scented, while those of *O. muricata*×*biennis* are pale and faintly scented.

This difference between the reciprocal hybrids is also clearly manifest in the crosses of *O. Lamarckiana* with the types of our dunes. The *O. Lamarckiana*×*biennis* has been described in my *Mutationstheorie* (**2**:31) for two generations, the third having only been cultivated in 1907. The *O. Lamarckiana*×*muricata* has been described and figured in the same volume (see page 29), but I have not as yet succeeded in getting a second generation, partly on account of the weakness of the type and partly on account of the general phenomenon of strongly diminished fertility in all these primrose hybrids.

The reciprocals of the two hybrids just mentioned afford the curious and rare phenomenon which I call that of the *twin hybrids*. In crossing one spike of *O. biennis* with the pollen of one plant of *O. Lamarckiana*, one does not get one but two hybrid types. The same holds good for *O. muricata*. These forms are intermediates between the parents and almost alike when seen from a distance, but sharply distinguished when closely examined. These differences are the same whether *O. biennis* or *O. muricata* is the mother plant, the hybrids showing their divergent origin only in apparently subordinate marks. One of the twins has broad and flat leaves of a bright green; I call it *O. laeta*. The other has narrow, more or less furrow-shaped leaves of a grayish green, which are more hairy, and is therefore designated *O. velutina*. These same names may be used to distinguish the twins in all the hybrid combinations in which they may occur.

The twin hybrids, *O. laeta* and *O. velutina*, occur in numerous hybrid combinations where *O. Lamarckiana* or one of its mutants is the pollen parent; as for instance with *O. brevistylis*, *O. rubrinervis*, and *O. nanella*. In these cases they drop, at least in the first generation, the special mark of the mutant-father, and so are the same in all the cases named. The mother plant may be *O. biennis, O. biennis cruciata* (a form of *O. biennis* with linear petals which occurs in the dunes of Holland), *O. muricata,* or some other species of Onagra, although not all of them are capable of producing twins.

In the cases named the twins are widely different from their reciprocal hybrids, but closely related between themselves. Their characters often show transgressive fluctuability, and as a result of this they are more easily distinguished at some periods of their life than at others. The better the culture and the stouter the plants, the larger and more striking are the differences. Especially specimens which contrive to make a large rosette of root leaves before they send up their stem, and therefore begin flowering only late in the fall, are liable to display their differential marks in a most striking manner.

The twins are usually produced from the same cross in about equal numbers. On account of their highly diminished fertility it is difficult to get large cultures of their progeny, for even when the pods are large and contain an apparently full supply of seed, the germinating percentage is often very small. The following figures, however, will suffice to state the fact.

TABLE I

O. LAETA AND O. VELUTINA IN FIRST GENERATION

Mother	Father	Number of progeny	Percentage of laeta	Percentage of velutina
O. biennis	×O. brevistylis	85	47	53
O. biennis	×O. rubrinervis	50	42	58
O. b. cruciata	×O. brevistylis	91	48	52
O. muricata	×O. Lamarckiana	58	61	39
O. muricata	×O. brevistylis	120	59	41
O. muricata	×O. nanella	59	58	42
	Average		52	48

In this experiment the parents have been those described above, and the crosses have been made by myself in the summer of 1905. The countings have been made during the flowering-season of 1907, only a small part of each of the cultures having remained rosettes; but the distinguishing marks in these were as evident in the fall, as those of the flowering plants. Some crosses, tried in previous years, had given the same results and prepared the method for an exact counting.

In the young plants, before the sending-up of the stems, it is of course easy to count far larger numbers of plants, but the influence of transgressive fluctuability is somewhat greater. I counted for *O. biennis×brevistylis* 287, for *O. biennis×Lamarckiana* 347, and for *O. biennis cruciata×brevistylis* 208 seedlings, and found 55 per cent., 60 per cent., and 64 per cent., or on an average 60 per cent. specimens of *O. velutina*, the remaining 40 per cent. being *O. laeta*. The figures, although from the cause given not as exact as those given above, evidently confirm the result.

Tried in the second generation, from artificially and purely self-pollinated seed, each of the twins yields a uniform progeny, with exactly the same characters as its parent. Therefore they may be considered as constant hybrid races. I made the majority of the crosses of the following table in 1903; had the first generation, which often consisted of only a few specimens on account of the diminished fertility, in 1905; and counted the forms in the second generation during the flowering-period of 1907. Most of the plants were counted in full flower, some of them, however, in the condition of rosettes of root leaves. Only for *O. muricata×brevistylis* the cross was made in 1905 and the second generation grown in 1906.

TABLE II

CONSTANCY OF O. LAETA AND O. VELUTINA IN SECOND GENERATION

Cross	First generation	Second generation	
		laeta	velutina
O. biennis×Lamarckiana	laeta	13	0
	velutina	0	9
O. biennis cruciata×Lamarckiana	laeta	19	0
	velutina	0	3
O. muricata×Lamarckiana	laeta	4	0
	velutina	0	53
O. biennis×rubrinervis	laeta	30	0
	velutina	0	6
O. biennis cruciata×rubrinervis	laeta	22	0
	velutina	0	3
O. muricata×brevistylis	laeta	34	0
	velutina	0	57
Total		122	131

I also tried this result by counting seedling plants as soon as they clearly showed their differentiating marks. From *O. laeta* seed I got only *laeta;* from *O. velutina* seed only *velutina.* The observed cases for *O. laeta* were: *O. biennis*×*rubrinervis* (150), *O. biennis cruciata*×*Lamarckiana* (18), the same×*O. rubrinervis* (143); and for *O. velutina*, *O. muricata*×*Lamarckiana* (126), the same×*O. rubrinervis* (195), and the same×*O. brevistylis* (190). The figures in parentheses show the numbers of seedlings observed; together they give 311 seedlings of *O. laeta* and 511 of *O. velutina.*

It should be stated here that in the cross between *O. muricata* and *O. brevistylis* the character of the last-named species followed the Mendelian law in the case of both of the twins. The 34 *O. laeta* contained 30 per cent., and the 57 *O. velutina* 21 per cent., together also 26 per cent., of short-styled individuals, which bore in their leaves and flower-buds and in the flattened lobes of their stigma all the characteristics of their male grandparent. The *O. brevistylis* character is thereby shown to be independent of the hereditary units which cause the production of the twins.

The third and fourth generations have been cultivated in only one case, as yet, which was a cross made between *O. muricata* and the pollen of *O. Lamarckiana* in 1901. The *O. laeta* in this case was entirely sterile, and so only the *O. velutina* could be studied. It gave a constant progeny of small extent, the fertility in artificial self-pollination remaining in a diminished condition.

TABLE III

CONSTANCY OF O. VELUTINA DURING FOUR GENERATIONS

Cross of O. muricata×O. Lamarckiana

Generation	O. laeta	O. velutina	O. laeta from O. velutina
Cross, 1901	—	—	—
1st generation, 1902	35 (sterile)	35	—
2nd generation, 1903–4	—	27	0
3rd generation, 1905	—	53	0
4th generation, 1907	—	60	0

All in all 175 plants were observed, all bearing the same characters.

The phenomenon of twin hybrids seems to be very rare in plants. There can be do doubt that its occurrence in *Oenothera Lamarckiana* is intimately connected with at least part of the special manner in which this species displays its mutability. The production of some of the mutants seems to be quite dependent upon it, though that of others is independent. But I must reserve an account of my experiments on this point for another occasion.

SUMMARY

1. Hybrids between members of the group Onagra or the *O. biennis* group of the evening primroses are, as a rule, constant in succeeding generations. An exception is *O. brevistylis*, the character of which follows MENDEL'S law.

2. The reciprocal hybrids of this group are, as a rule, unlike one another, and mostly patroclinous.

3. In many cases, where *O. Lamarckiana* or one of its derivatives is the father, two forms of hybrids are produced instead of one. These forms may be called twin hybrids.

4. One of the twins is broad and smooth-leaved and is called *O. laeta;* the other is more hairy and has furrow-shaped leaves, and is designated as *O. velutina.*

5. *O. laeta* and *O. velutina* are produced by the combinations *O. biennis*×*Lamarckiana* and *O. muricata*×*Lamarckiana,* and by those of some of their derivatives.

6. They are produced in about equal numbers.

7. They remain constant in the second generation. In the only ascertained case they also showed themselves so in the following generations.

AMSTERDAM

A CONTRIBUTION TOWARD A KNOWLEDGE OF THE GENUS WASHINGTONIA

S. B. PARISH

(WITH TWELVE FIGURES)

"We followed the sandy bed of the Carriso nearly all day at a snail's pace, and at length reached the 'little pools,' where the grass was luxuriant, but very salt. This valley is at no point more than half a mile wide, and on each side are mountains of gray granite and pure quartz. A few miles from the spring called 'Ojo Grande,' at the head of the creek, several scattered objects were seen, projected against the cliffs, hailed by the Florida campaigners, several of whom were along, as old friends. They were cabbage trees, and marked the *locale* of a spring, and a small patch of grass."

In these words we have the record of the discovery of the Washington palm. The date was November 28, 1846, and the discoverers were the party of the military reconnoissance under Major W. W. EMORY, now nearing the end of their long journey, through unexplored mountains and arid deserts, from the Missouri River to San Diego.

Seven years later a company of surveyors under W. P. BLAKE, engaged in exploring a route for the projected Pacific Railroad, entered the Colorado Desert through the San Gorgonio Pass, on their way to Fort Yuma, the route now followed by the Southern Pacific Railway. On November 15, 1853, they reached a little nook, nestled under the shadow of rugged San Jacinto Mountain, which afterward came to be known as Agua Caliente, and more recently as Palm Springs. "A growth of rushes," says the itinerary, "forms a narrow margin of green vegetation around the spring and its outlet. Willows and mesquite bushes grow there also, and I found a young palm tree, spreading its broad, fan-like leaves among them. The surrounding desert and the palm tree gave the scene an oriental aspect." Hidden in nearby canons were groves of some of the noblest palms of the whole desert region, but the travelers passed on unaware of their presence.

Dr. C. C. PARRY has recorded (**'81**) that he also became acquainted with the desert palms in 1849–1850, while botanist of the Mexican Boundary Survey. But in the introduction to the *Botany* of the boundary he made no mention of these notable trees, while enumerating so many of the remarkable plants of the Colorado Desert. Neither do they find a place in the body of the volume; nor are they mentioned by the botanists who reported upon the collections of the Pacific Railroad Surveys.

Not until 1861 did they receive botanical recognition, and was an attempt made to assign them a systematic position. In that year Dr. J. G. COOPER published (Smithsonian Report for 1860) the names of certain trees "omitted, by an oversight, from a list of those on the Mexican boundary" which had appeared in a preceding report. Last on the list appears "Brahea? dulcis? Mart." COOPER had leaves, collected, he states, by Dr. SUTTON HAYES, at Palm Springs[1] and he notes their thready segments and prickly petioles, and states that the fruit is edible.

The matter rested here for eleven years more, when the attention of European botanists was attracted to some young palms grown at Ghent, by the enterprising house of LINDEN, from seed reported to have come from the arid interior of our Pacific coast. At first they were thought to belong to Brahea or to Prichardia, but in 1879 Dr. H. WENDLAND, the most eminent palmographer of the time, became convinced of their generic distinctness, and gave the name Washingtonia, "in honor of the great American," to the palms which, he says, had been known in gardens as *Brahea* or *Prichardia filifera*.

THE GENERIC NAME

It appears, however, that there had been some previous suggestions as to the bestowal of the name of Washington upon certain other plants. A Dr. WINSLOW had proposed that the Californian Sequoias might fitly bear that honored name. For this reason SUDWORTH, in 1897, proposed ('97) to substitute for WENDLAND'S name the cacophonous chloronym *Neowashingtonia*. In this he has been followed by some American nomenclaturists, but not by European palmographers.

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[1] Probably not the Palm Springs of BLAKE's Report. Dr. HAYES accompanied as assistant surgeon the government expedition which in 1858–59 surveyed an emigrant route from El Paso to Fort Yuma. Later he made some botanical collections near San Diego, and probably traveled to that town from Fort Yuma by the same road taken by EMORY's party, the customary route at that time. This "Palm Springs" may well have been that of EMORY. There is a sketch of Dr. HAYES's life in Seeman's Jour. Bot. **1**:254. 1863, and substantially the same account in Biologia Cent.-Am. Botany **4**:153.

In the same year BRITTON and BROWN[1a] transferred the umbelliferous plants commonly known as Osmorrhiza to *Washingtonia* Raf., a disposition subsequently accepted, with confessed reluctance, by COULTER and ROSE.[2]

It would seem evident that one of the leading principles which should govern, if a stable nomenclature is to be attained, is that the code should not be interpreted in the interest of novelty. Changes of name should be made only on clearest evidence of their necessity, and in all cases of reasonable doubt the name in possession should be left undisturbed. Tried by this standard it does not appear that either of these proposed changes is justifiable. WINSLOW'S alleged publication is valid neither in its character nor in its vehicle. It occurs in the course of a rambling popular account of a visit to the Sierra Nevada, published in the *California Farmer* of August 24, 1854, a farmer's weekly of the ordinary type. Possibly the original defect might be considered to have been cured by the quotation of some paragraphs of WINSLOW'S letter in an article on "The big tree," by HOOKER,[3] and by CARRIÈRE'S citation in the synonymy under *Wellingtonia gigantea*.[4] In any event, Washingtonia as a name for the Sequoias lapsed at once into hopeless synonymy, leaving it, under the International Rules of Botanical Nomenclature, open for subsequent use.

The facts in the other case are these. In 1818, in a review of PURSH'S *Flora*, RAFINESQUE remarks that, in his opinion, *Chaerophyllum Claytoni* Pers. had been incorrectly referred; and he continues: "Several names have been proposed for it, Washingtonia, Osmorrhiza, Gonantherus, but these are not yet published; the second

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[1a] BRITTON and BROWN, Ill. Fl. 2:530. 1897.

[2] COULTER and ROSE, Monog. Umbell. Contrib. U. S. Nat. Herb. 7:61. 1900.

[3] HOOKER, Jour. Bot. and Kew Garden Misc. 7:26 *et seq.* 1855.

[4] CARRIÈRE, Traité des Conifères, Ed. 2, 217. 1867.

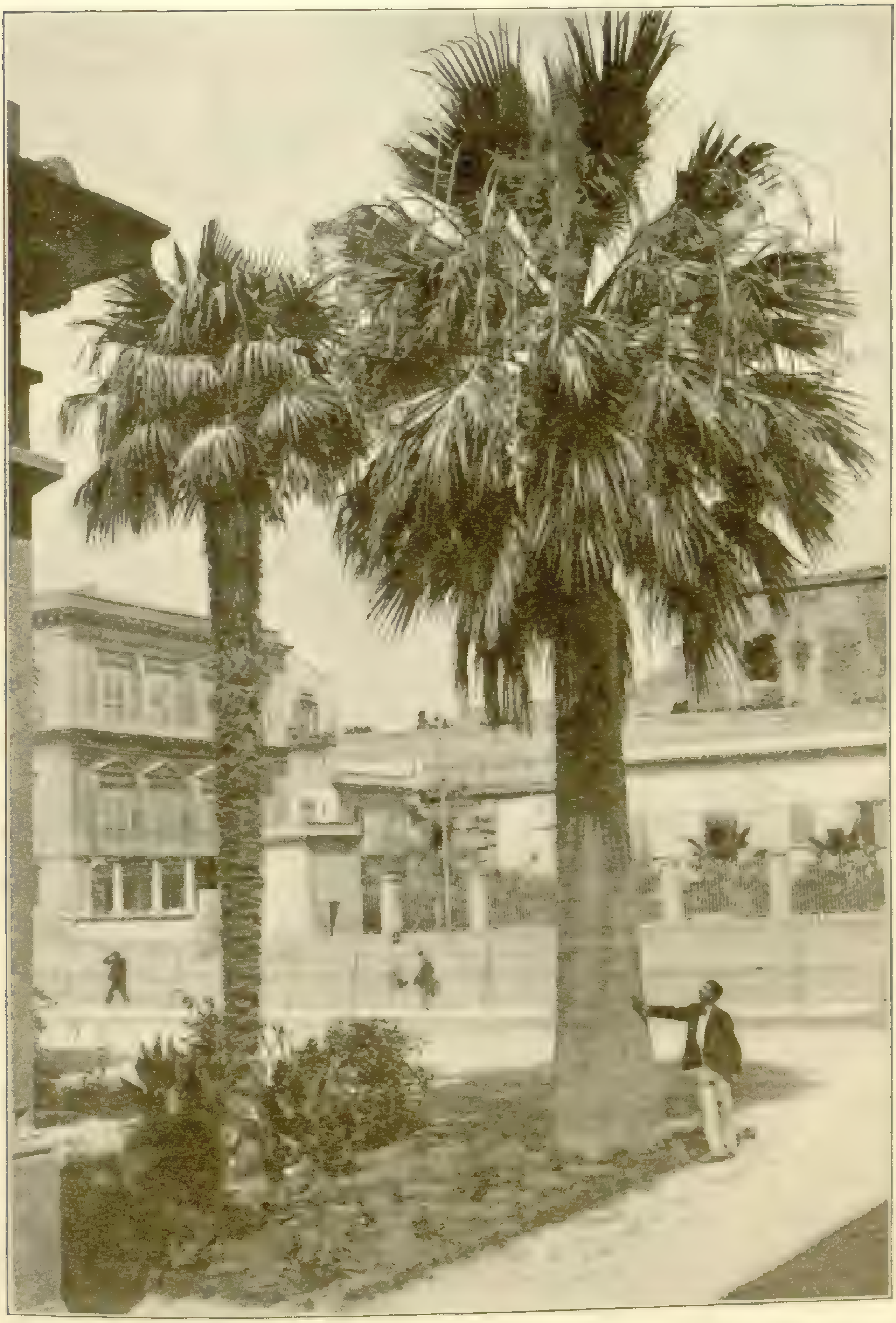

FIG. 1.—*W. filifera* Wendl. (the right-hand tree) in the Botanical Garden, Palermo, Italy.

is perhaps the best,"[5] and in the following year he did *publish* this second name.[6] In order that we may be enabled to make a confusing change in two familiar names, therefore, we must hold that Rafinesque published a name when he expressly disclaimed so doing, and did not publish it when he formally undertook the task.

NAME OF THE TYPE SPECIES

Here it is convenient to consider another nomenclatural question. Wendland's original species was published as *W. filifera;* but in his *Revisio*, Kuntze (**'91**) proposed to change it to *W. filamentosa*, on the ground of priority, citing in support "*Brahea filamentosa* Wendl. in Cat. Haage & Schmidt (1875), *Prichardia filamentosa* Wendl. ex Fenzi in Bull. Soc. Tosc. (April, 1876)." To seek in a tradesman's catalogue for a pretext for displacing an established name, requires a lust for change almost amounting to a mania. But if an appeal to trade-lists is to be made, priority is against the change, for Haage and Schmidt offered *Brahea filamentosa* in their autumn catalogue of 1875, but in the spring of the same year Linden in his list had put the same plant on the market as *Prichardia filifera* (Fenzi **'76**). *Prichardia filamentosa* of Fenzi's paper is a *nomen nudum*, being without a word of scientific description, or any reference to a published species. As the proper specific name, *filamentosa* has absolutely no standing.

THE SOURCE OF WASHINGTONIA FILIFERA

When we pass from the consideration of names, we find ourselves confronted by questions of greater difficulty. What precisely was the palm variously known to gardeners and seed-dealers as *Brahea filifera* or *Prichardia filamentosa*, and to which Wendland gave the name *Washingtonia filifera*, and whence came it? Wendland had before him a few[7] young trees which had been grown in the palm-

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[5] Am. Month. Mag. **2**:176. 1818. This publication is invalid under the Laws of Nomenclature formulated by the Botanical Club of the A. A. A. S. See Canon 12 of the latest revision of that code, in Bull. Torr. Bot. Club **34**:171. 1907.

[6] Jour. Phys. **89**:257. 1819.

[7] There could have been but few of these trees, for, in a letter to the writer, M. Lucien Linden, the present head of the house, writes: "Vers 1872 mon père a reçu d'un dizaine des graines de ce palmier qu'il avait rapporté d'un voyage en Californie." In his original description Wendland states that it was introduced by Linden in 1869, but this is evidently an error.

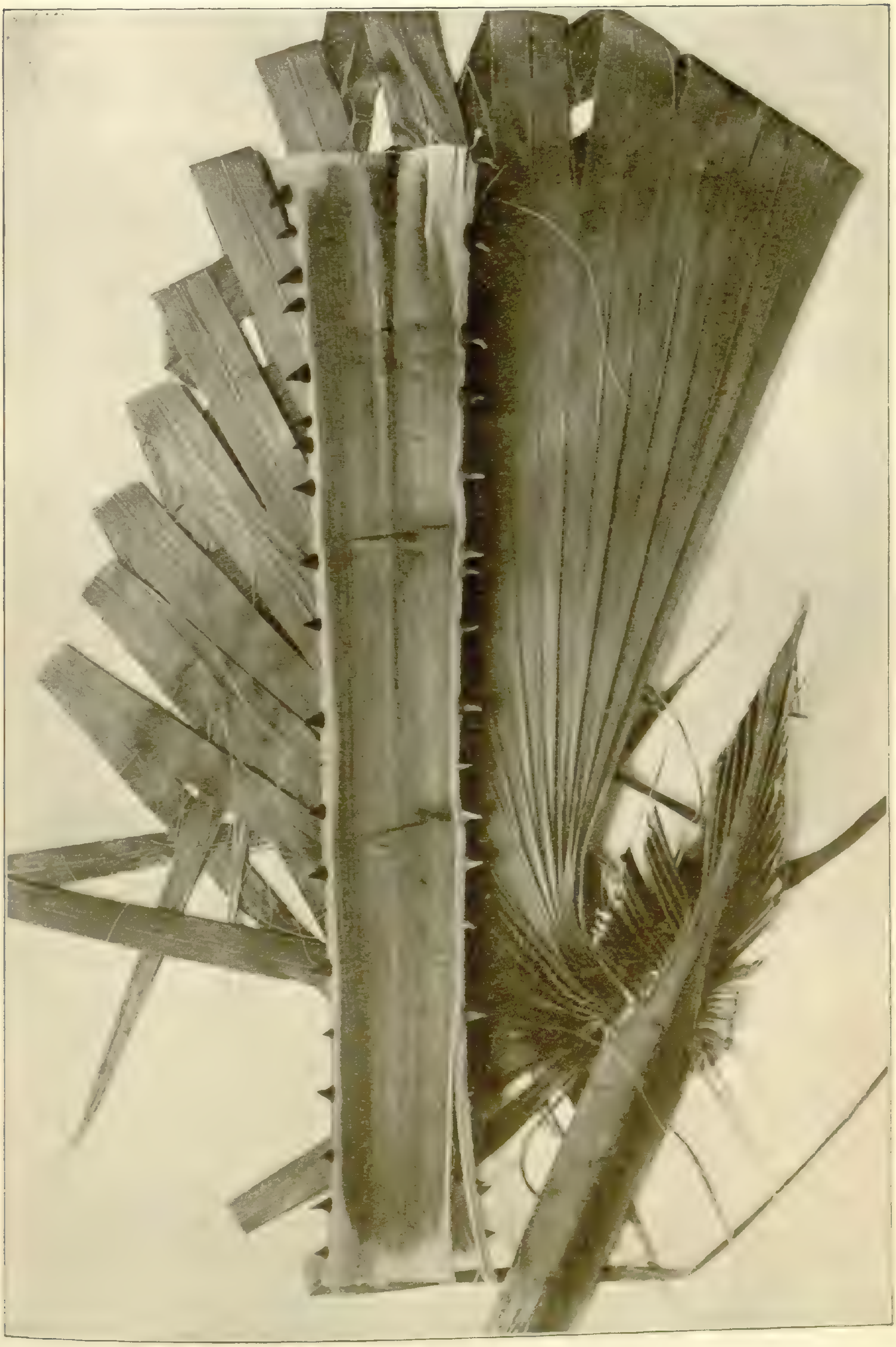

FIG. 2.—A leaf from the tree shown in *fig. 1*.

houses of LINDEN in Ghent. It seems certain that the seeds were brought to Europe by ROEZL.[8] They purported to have been collected in Arizona, near the Colorado River, and FENZI ('76)[9] even gives latitude and longitude, which would locate the parent trees in the neighborhood of Prescott, Arizona, a region rather of pines than of palms. Definite as are these statements, it is impossible that ROEZL ever could have seen a Washingtonia growing spontaneously or have collected its seed. The seeds which he carried to Europe he must have received from another, probably in San Francisco, and with them an inaccurate or misunderstood account of their source.

ROEZL appears to have made but a single visit to America. He left Europe in August 1872, landing at New York, and proceeding by way of St. Louis to Denver, where he made his headquarters. On September 6 he wrote from that place that he had sent home six boxes of *Yucca angustifolia*, some cactuses, and bulbs of Calochortus. He then made a trip, of a fortnight's duration, into northern New Mexico, where he saw *Abies concolor*, *Yucca baccata*, and *Ipomoea leptophylla*. On October 3 he wrote from San Francisco, telling of his route, by the Union and Central Pacific Railways, through Utah and Nevada. He remained in San Francisco until about November 1, when he sailed for Panama.[10]

The early reports of the location of the parent trees proving unreliable, we are left without any authentic information as to the source of LINDEN'S seeds. They may have come from native trees in the region now known to be occupied by these palms, or from some of the older cultivated trees in southern California. There is reason to believe that some of the earliest subsequent importations of seed were collected by the late GEORGE W. DUNN in Cantillas Cañon, on the desert borders of northern Lower California.

[8] "Es ist nämlich von RÖZL, in Nord-Mexico, bei Arizona, am Rio Colorado, eine Corephine gesammelt worden, welche unter dem Namen *Prichardia filamentosa* jetzt in den Handelgärten gezogen wird" (DRUDE '76).

[9] "La scopeta di questa Palma se debba all' intrepide B. ROEZL, che l'aviabbe retrovata nell' Arizona (Stati Uniti), dove cresca spontanea sulle rive del Colorado, a circa 115° de longitudine ouest del meridiano de Parigi, e circa de 35° latitudine nord."

[10] Notices of ROEZL may be found in Gartenflora **1874**:49; **1889**:330; Jour. Bot. **1874**:384; Gard. Chron. **2**:521. 1889. He died at Prague, October 14, 1889. at the age of 61 years.

WASHINGTONIA ROBUSTA

If we turn from this fruitless attempt to trace the indigenous origin of WENDLAND'S *W. filifera* to his description of that plant, we find it unsatisfactorily vague, as is also the later characterization of his second species, *W. robusta;* while among writers and cultivators there exists great confusion and misapprehension as to the identity of the two species.

This second species WENDLAND ('83) founded on young plants grown by VAN HOUTTE at Ghent, and its ascribed indigenous source is manifestly apocryphal, since it was asserted to be "the borders of the Sacramento River." VAN HOUTTE received the seeds under the name of the species already known, and under that name their product was at first sold, until WENDLAND recognized them as distinct, and published the name *W. robusta* (ANDRÉ '95).

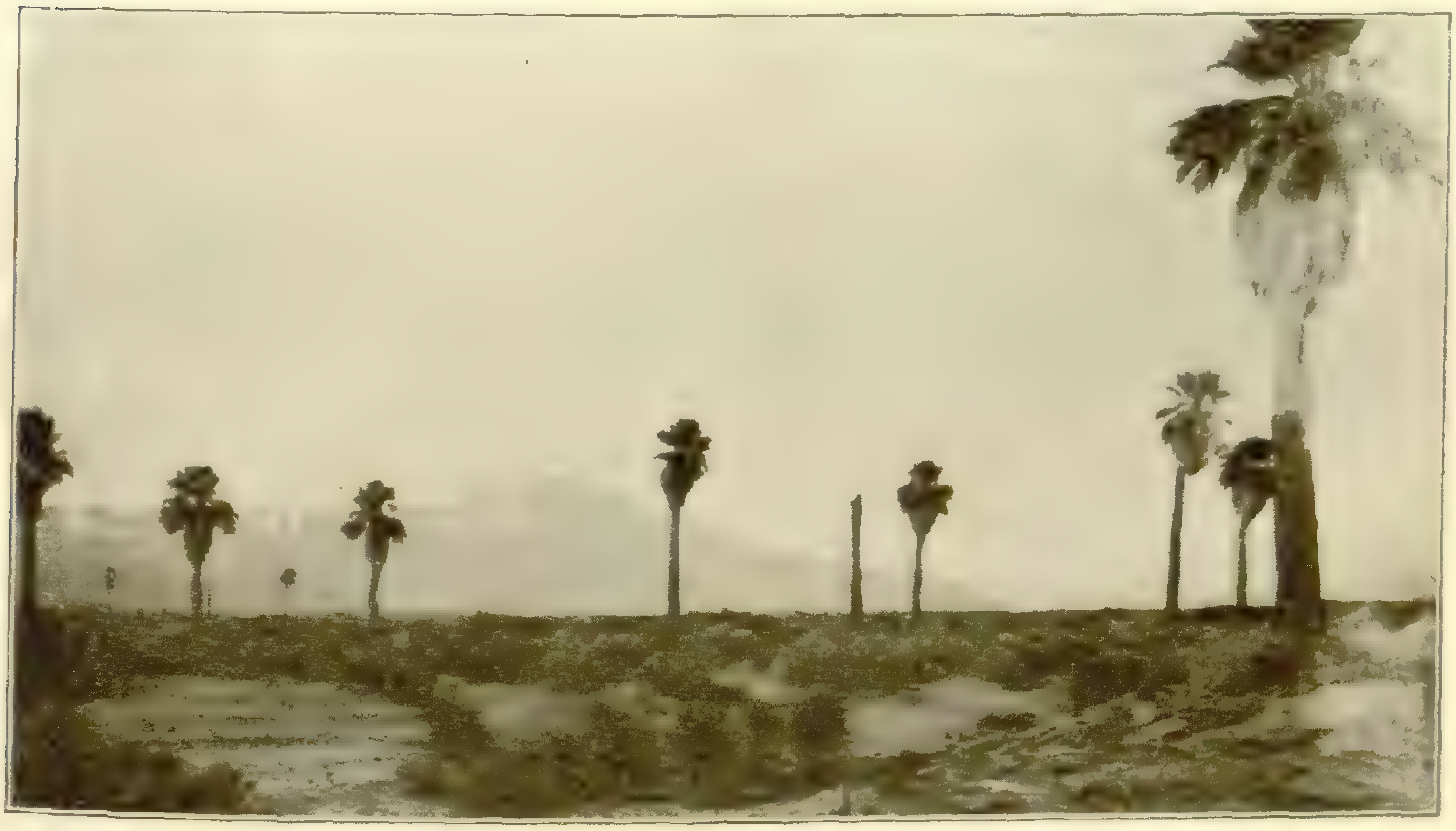

FIG. 3.—*W. filifera* var. *robusta* (Wendl.) Parish; very old trees at the western margin of the ancient lake bed, Colorado Desert.

It is significant that about this time collectors began to secure palm seed at Palm Springs, in the Colorado Desert. I am convinced that this place was the true source of WENDLAND'S second type. Certain it is that the trees growing there are identical with those now recognized in Europe as representing that species. It was on material from this station that WATSON ('80) based his characterization of the genus and of *W. filifera*, the first formal and satisfactory description of either genus or species.

CONFUSION RESPECTING THE SPECIES

From what has now been stated it will be understood that confusion might readily arise as to the identity of these two species. Each was insufficiently described from young plants growing under glass; and the indigenous source of each was either misapprehended or misrepresented. Added to this is the undoubted fact that soon after the publication of the second species, certain dishonest dealers were accustomed to fill orders for either from the same drawer, the only difference being in the price. Moreover, in recent years, through honest misunderstanding, the seeds supplied to the market as "true *W. robusta*" belong in reality to an undescribed species. Naturally the product of these falsely named seeds adds to the confusion. It happens, therefore, that neither of the palms known in California as *W. filifera* and *W. robusta* bears its true name.

A clue in these difficulties would be found could we ascertain exactly what was WENDLAND'S *W. filifera*, but this seems impossible. The only practical course is to accept as representing this species certain mature trees growing in the Riviera, which are recognized by European authorities as authentic specimens of WENDLAND'S two palms. They are distinguished by a character which does not appear in either of the original descriptions, and one too marked, it would seem, to have been overlooked. Yet in the native groves of the desert, where it is to be seen, it has been overlooked by the many accomplished botanists who have visited them. While not entirely satisfactory, this seems the best disposition attainable, and I have adopted it in the following key, which represents my present understanding of the genus.

KEY TO WASHINGTONIA

- Petiole acuminately prolonged in the blade.
  - Blade abundantly filiferous.
    - Margins of the petiole unarmed near the blade......1. *W. filifera.*
    - Margins of the petiole armed throughout........1*a*. *W. filifera robusta.*
    - Margins armed only near the base........1*b*. *W. filifera microsperma.*
  - Blade destitute of filaments or nearly so..................2. *W. gracilis.*
- Petiole obtuse at junction with the blade......................3. *W. sonorae.*

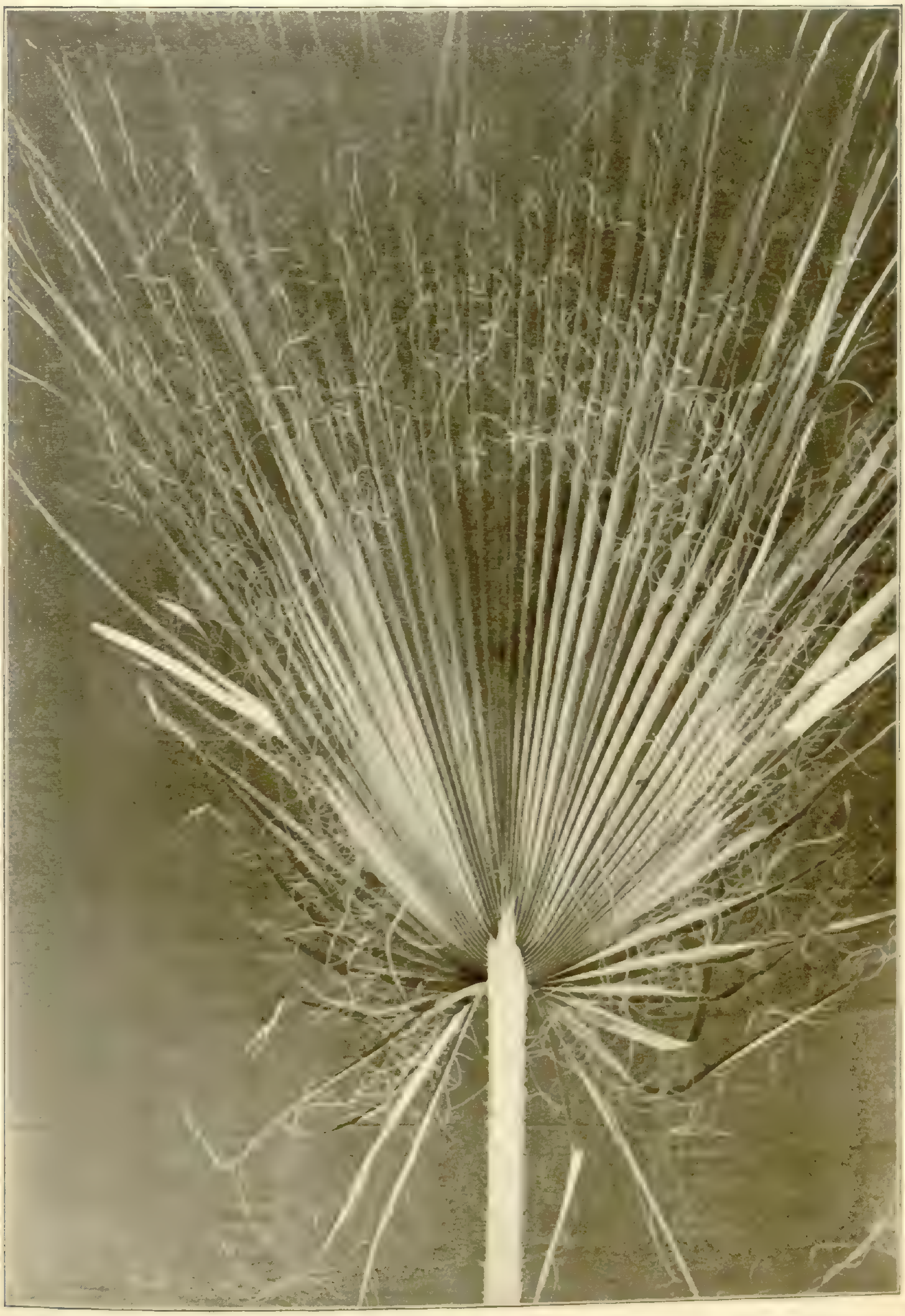

FIG. 4.—Leaf of *W. filifera robusta*, from a cultivated tree at San Bernardino, California.

1. **Washingtonia filifera** Wendland, Bot. Zeit. **37**:68. 1879.—*Figs. 1, 2.*

Margins of the petioles armed to the middle, or somewhat higher, naked above; otherwise as in the following variety, so far as known.

There seems to be no reason for selecting this form as representing Wendland's species except that European palmographers so regard trees having this character which are growing in the Riviera. There are some trees thus armed growing in the native groves at Palm Springs, and they appear not to differ otherwise from the fully armed ones. In the same groves there are also young palms, probably five or six years old, having petioles without the usual corneous margin, and armed only with weak prickles, or nearly destitute even of these. No mature trees of this kind were seen. A similar difference is

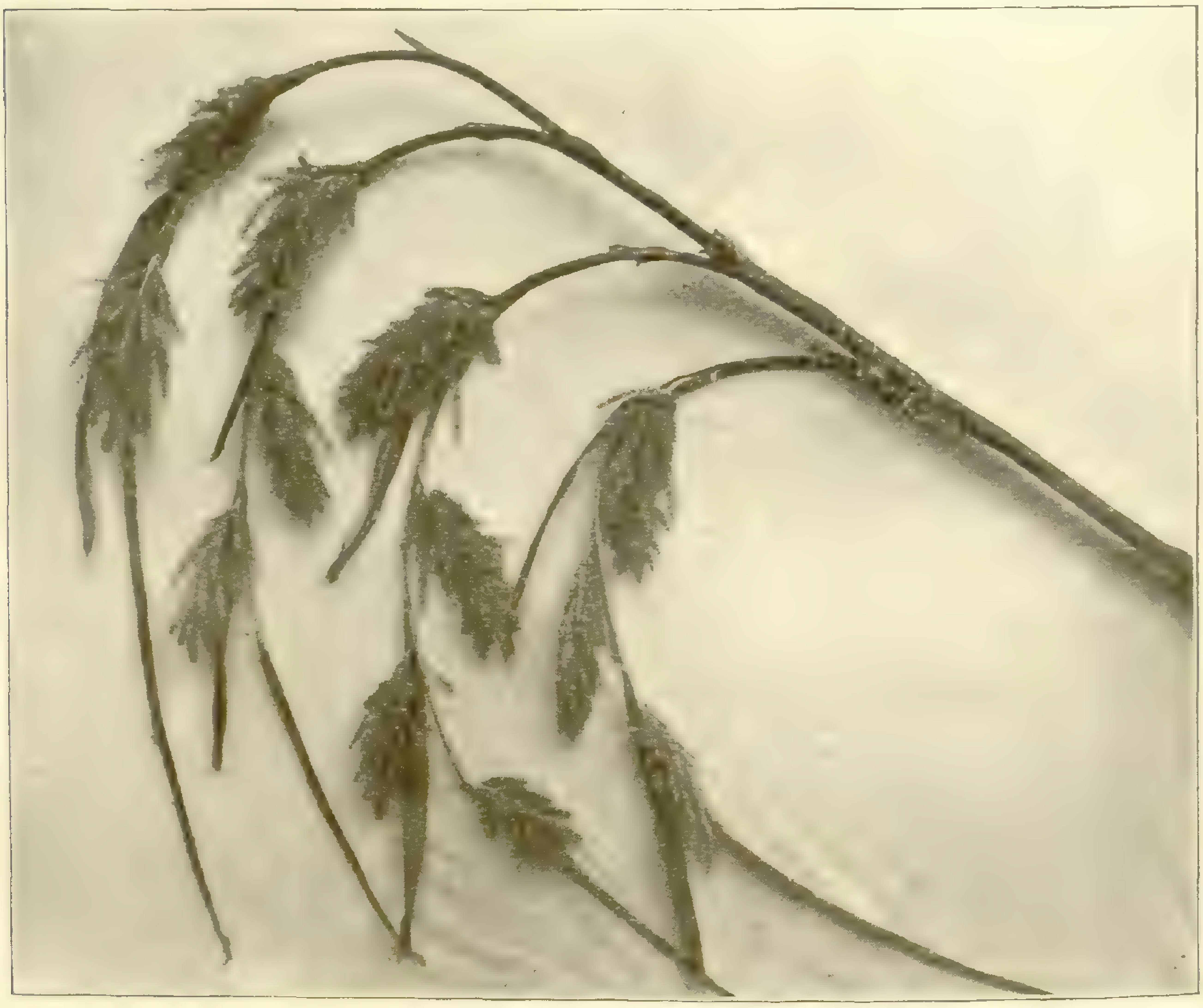

Fig. 5.—Panicle, in full flower, of *W. filifera robusta*, from a cultivated tree at San Bernardino.

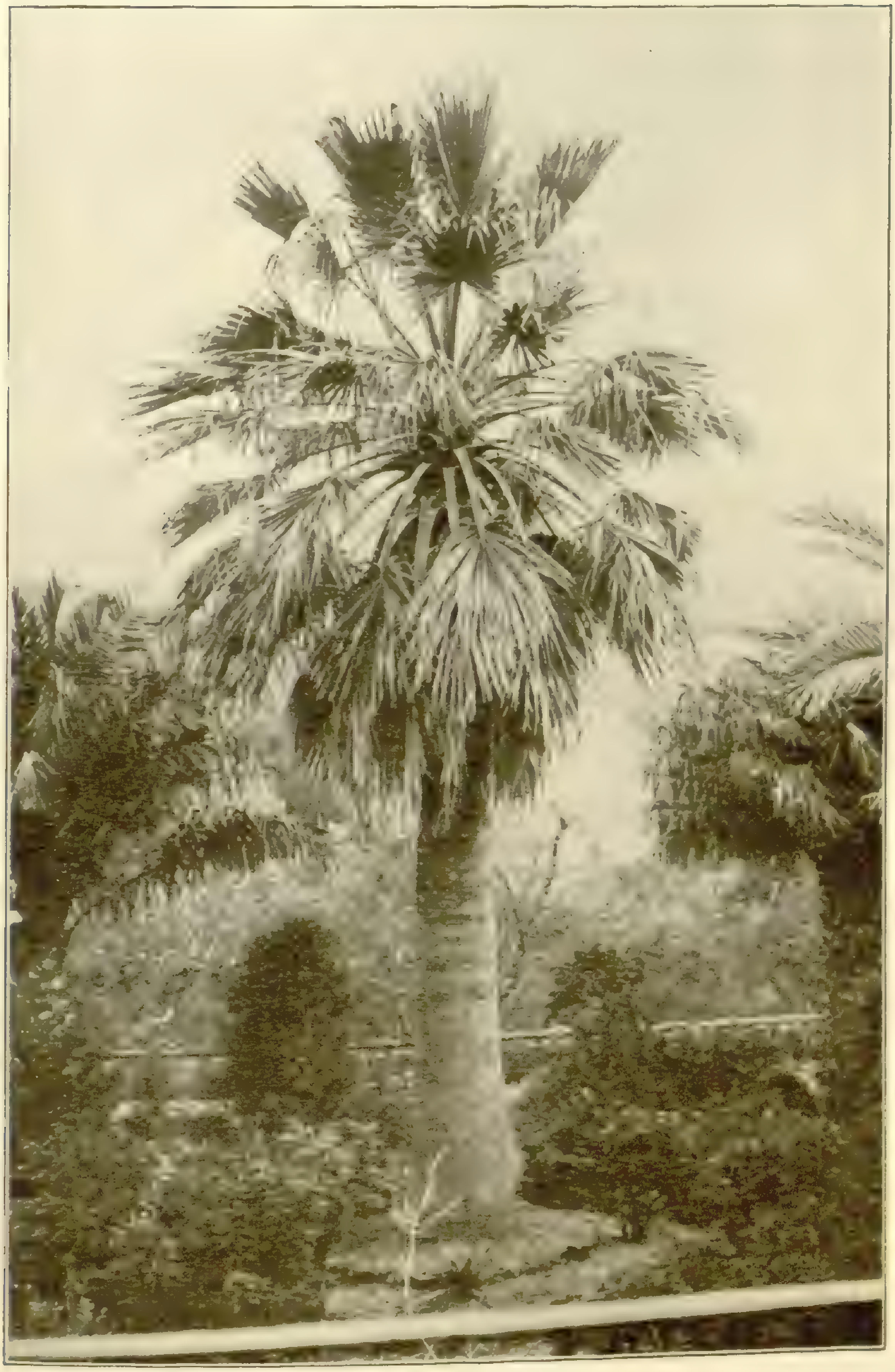

FIG. 6.—*W. filifera* var. *microsperma* Beccari; in the gardens of Count Parravicino, Campo Romano, near Viareggio, Tuscany. This tree was planted in 1878, when 4–5 years old, and flowered for the first time in 1902.

reported in the armature of the petioles of *Erythea edulis*, some trees having naked petioles, while others show rudimentary spines.

1*a*. WASHINGTONIA FILIFERA Wendl. var. **robusta,** n. comb.—*W. robusta* Wendland, Garten Zeit. **2**:198. 1883; *W. filifera* S. Watson, Bot. Cal. **2**:211, 485. 1880, and of American gardens; *W. filamentosa* Kuntze, Rev. Gen. Pl. **2**:737. 1891; Sargent, Sylva **10**:47. *pls. 5–9.* 1891; *Neowashingtonia filamentosa* Sudworth, U. S. Dept. Agr., Div. For., Bull. **14**:105. 1891.—*Figs. 3–5.*

Trunk stout, enlarged at the base, 20–27^{m} tall: petioles stout and until old erect, 1–1.5^{m} long, 1–1.25^{dm} wide at the dark-brown base, and one-half as wide at the blade; the upper surface concave, its thin, light-brown margins corneous and armed for their entire length with stout hooked spines, acuminately prolonged into the blade; ligule papyraceous, acuminate, lacerate, 2–5^{cm} long; blades 1–1.5^{m} in diameter, the 60–70 folds deciduously tomentulose on the lower edges, cleft two-thirds to the base, the margin of the divisions abundantly filiferous: panicle declined, exceeding the leaves, the primary branches 4–5, each bearing 2–5 separated thryses, which are exceeded by their ligulate, chartaceous, spathoid bracts; infloresence dense, but becoming diffuse in fruit: seed excavated on the raphal face.

Borders of the Colorado Desert of southern California, at low altitudes, seldom exceeding 350^{m}.

The flowers and fruit have been well described by WATSON. The flowers are copiously nectariferous, and exhale a heavy odor, disagreeable when near by, but when diffused somewhat suggestive of the perfume of orange blossoms.

1*b*. WASHINGTONIA FILIFERA Wendl. var. **microsperma** Beccari in litt., n. var.—*Figs. 6, 7.*

"A smaller tree, margins of the petioles armed only at the base." Differing in these respects only from the preceding.

Growing in the Riviera, but as yet not noticed in the natural groves.

2. **Washingtonia gracilis,** n. sp.—*W. robusta* of California gardens, not of WENDLAND.—*Figs. 8–10.*

Trunk slender, at least 20^{m} tall: petioles rather convex on the upper surface, 7–10^{dm} long, about 1^{dm} wide at the brown base and one-half as wide at the blade, the corneous margins armed with short hooked yellow spines for the entire length, acuminately prolonged in the blade; ligule papyraceous, narrow, the margin entire; blade

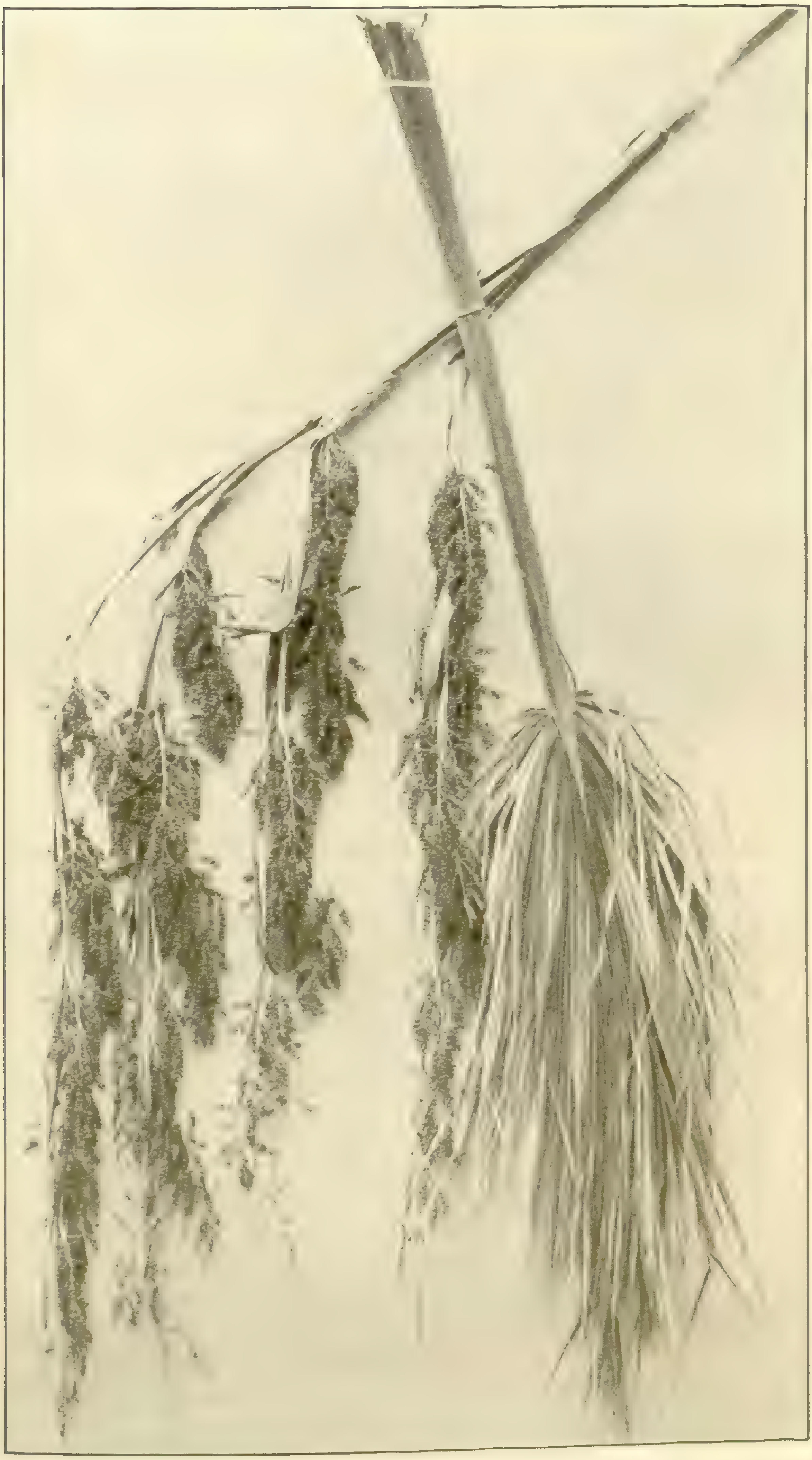

FIG. 7.—Leaf and very young fruit of *W. filifera microsperma;* from a tree in the gardens of Marquise Corsi, Sesto, near Florence, Italy.

8–10^{dm} in diameter, the folds 75–80, deciduously tomentose toward the base beneath, cleft little more than one-third toward the base, not filiferous except for an occasional single filament in the sinuses of some of the folds: peduncles declined, exceeding the leaves; primary divisions 6–8, each bearing 5–10 separated thryses, which are mostly exceeded by their narrow, deciduous, chartaceous bracts; flowers nearly sessile: calyx tubular-campanulate, 3^{mm} long, the short rounded lobes lacerate: tube of corolla 3^{mm} long, its lobes erect, narrowly lanceolate, 6–7^{mm} long: filaments subulate, 3^{mm} long, the versatile anthers 4^{mm} long: seeds broadly ovate, 6–7 by 5^{mm}, somewhat rugose on the raphal face.

Described from cultivated trees growing in San Bernardino and Riverside, California; probably indigenous in northern Lower California.

This palm is readily distinguished from *W. filifera* and its varieties by its slender trunk and smaller and less deeply divided leaves, which are without filaments and on shorter petioles. It is a tree of rapid growth and has been extensively planted in recent years in southern California, under the mistaken name of *W. robusta*, the true *W. robusta* being known as *W. filifera*. According to the report of a reliable dealer, the seed from which the older trees were grown was procured from indigenous groves in cañons, running to the sea, on the coast of Lower California, somewhere between the international boundary and Ensenada. Cultivated trees, which now have been fruiting for a number of years, are the present sources of the commercial seed. Much has been gathered from two noble trees, among the oldest in cultivation, which ornament the lawn of Mr. D. W. McLeod, of Riverside.

4. WASHINGTON SONORAE Watson, Proc. Am. Acad. **24**:79. 1889; **25**:136. 1890.—*Fig. 11.*

This species is readily separable from the others by the obtuse juncture of the petiole with the blade. I have seen only young plants, and their leaves are very abundantly filiferous.

The type station is given by WATSON as "in secluded cañons in the mountains about Guyamas." Dr. E. PALMER, the collector of the type specimens, informs me that the trees grew "in great quantities, and of great size, in the deep cañons running into the Gulf of California, far away from Guyamas." Dr. WATSON subsequently identified as of this species certain specimens collected by Dr. PALMER at La Paz, in Lower California, and on the opposite side of the gulf. The trees in cultivation have been grown, probably exclusively, from seed collected in San José del Cabo, in the same region of Lower California.

The natives of the Cape region recognize three distinct forms of *W. sonorae.* Two of these—"Palma Blanca" and "Palma Colorada"—are distinguished by

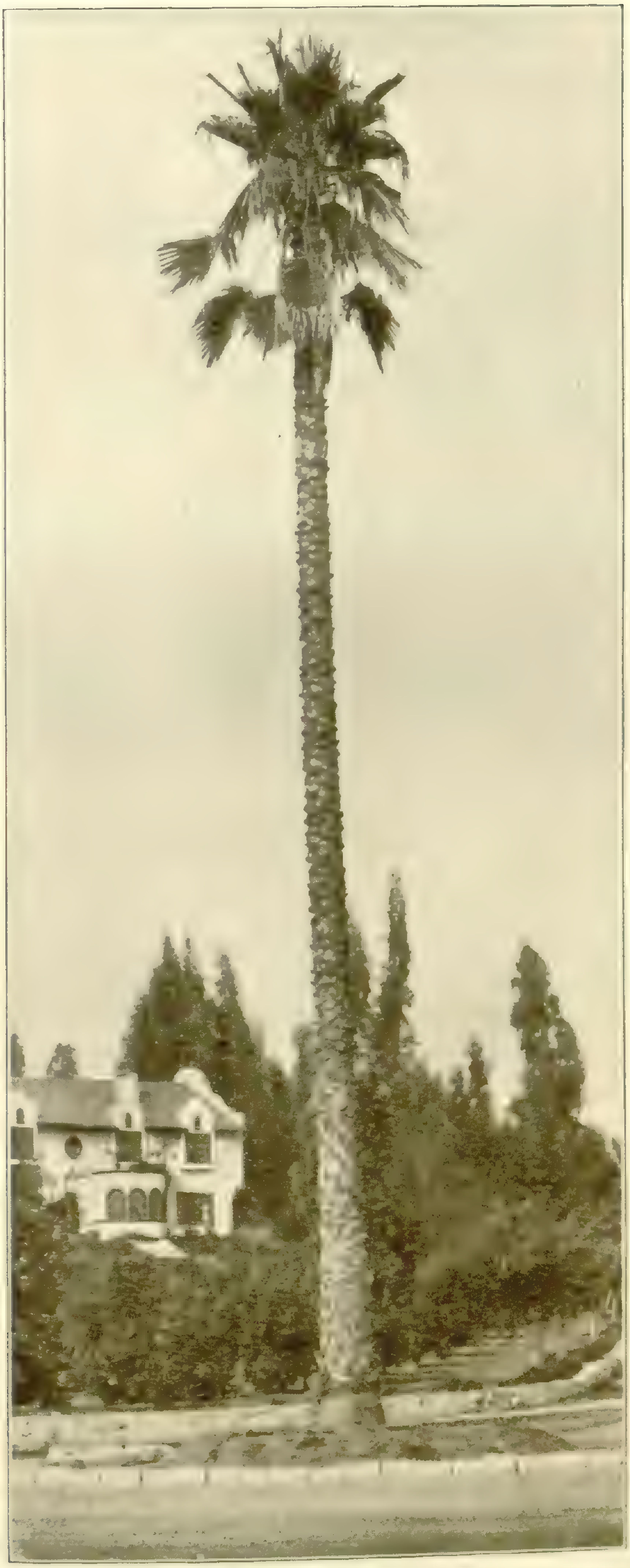

FIG. 8.—*W. gracilis* Parish; Victoria Avenue, Riverside, California. This tree is about 25 years old and 18^{m} high; its circumference at 5^{dm} from the ground is 15.75^{dm}; the leaves have been removed from the trunk.

the white or red color of the woody fiber of their trunks. The third—"Palma Nigra"—is said to be a smaller tree, growing at higher altitudes, where winter snows are not infrequent. Dr. FRANCESCHI, to whom I am indebted for this information, has grown many plants, at Santa Barbara, from seeds of each of these forms, but finds no differences in the young trees, nor am I able to detect any in the specimens he has kindly sent me.

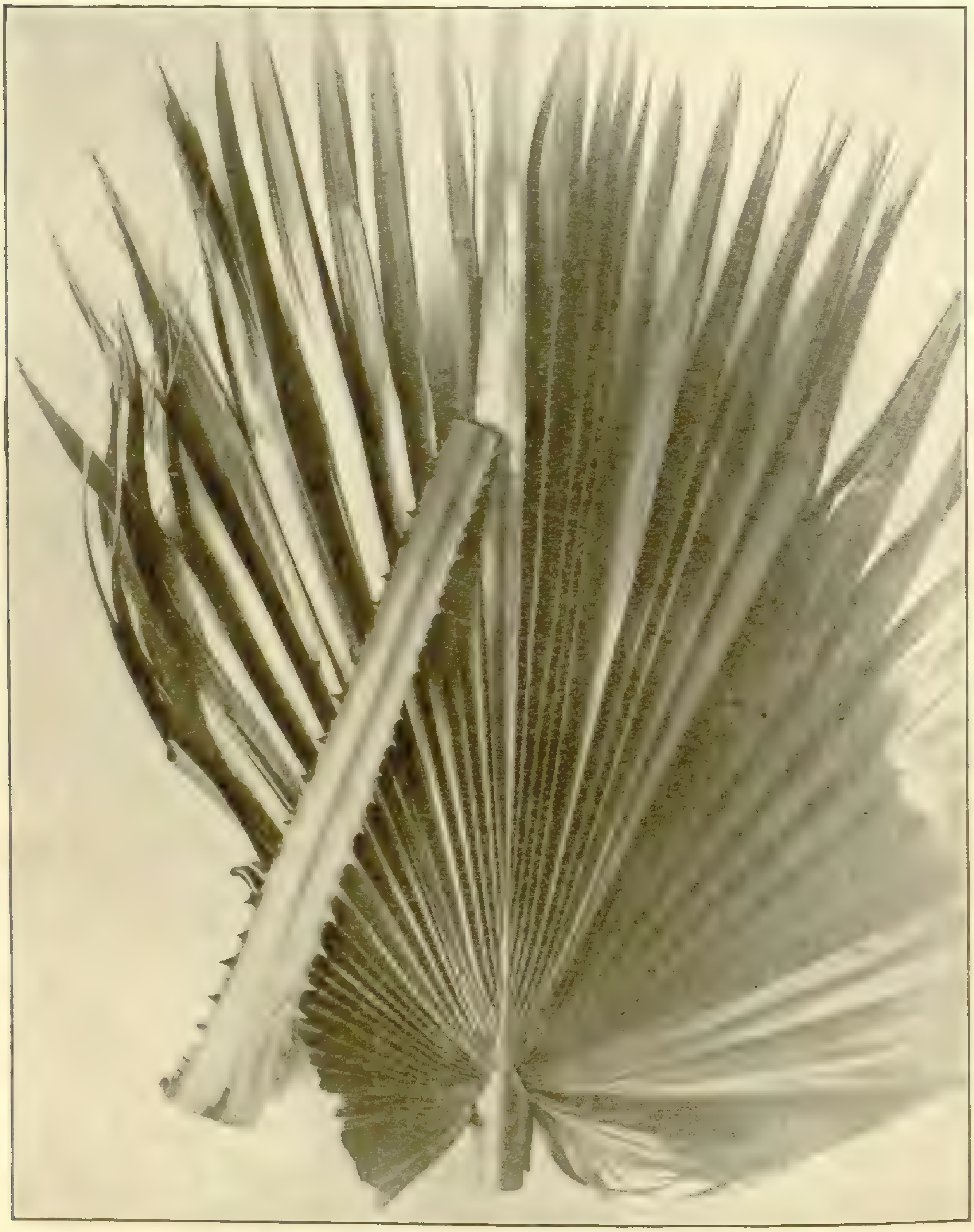

FIG. 9.—Leaf of *W. gracilis*, from a tree at the Santa Fé railway station, San Bernardino, California.

FRUIT AND SEED OF WASHINGTONIA

The fruit of Washingtonia is a small oblong drupe, black at maturity, with a thin, sweetish, rather dry pulp. The seed is brown, oblong to oblong-ovate, flattened, excavated or somewhat wrinkled on the raphal face. The first of these raphal characters seems to belong to *W. filifera* and its variety *microsperma*, the second to *W. filifera robusta* and *W. sonorae*, and the last to *W. gracilis*. To determine whether these characters are constant requires the study of extensive series of authentic seeds from varied sources. For this the material is not at hand. *Fig. 12*, for which I am indebted to Dr. Beccari, represents the seed as at present understood.

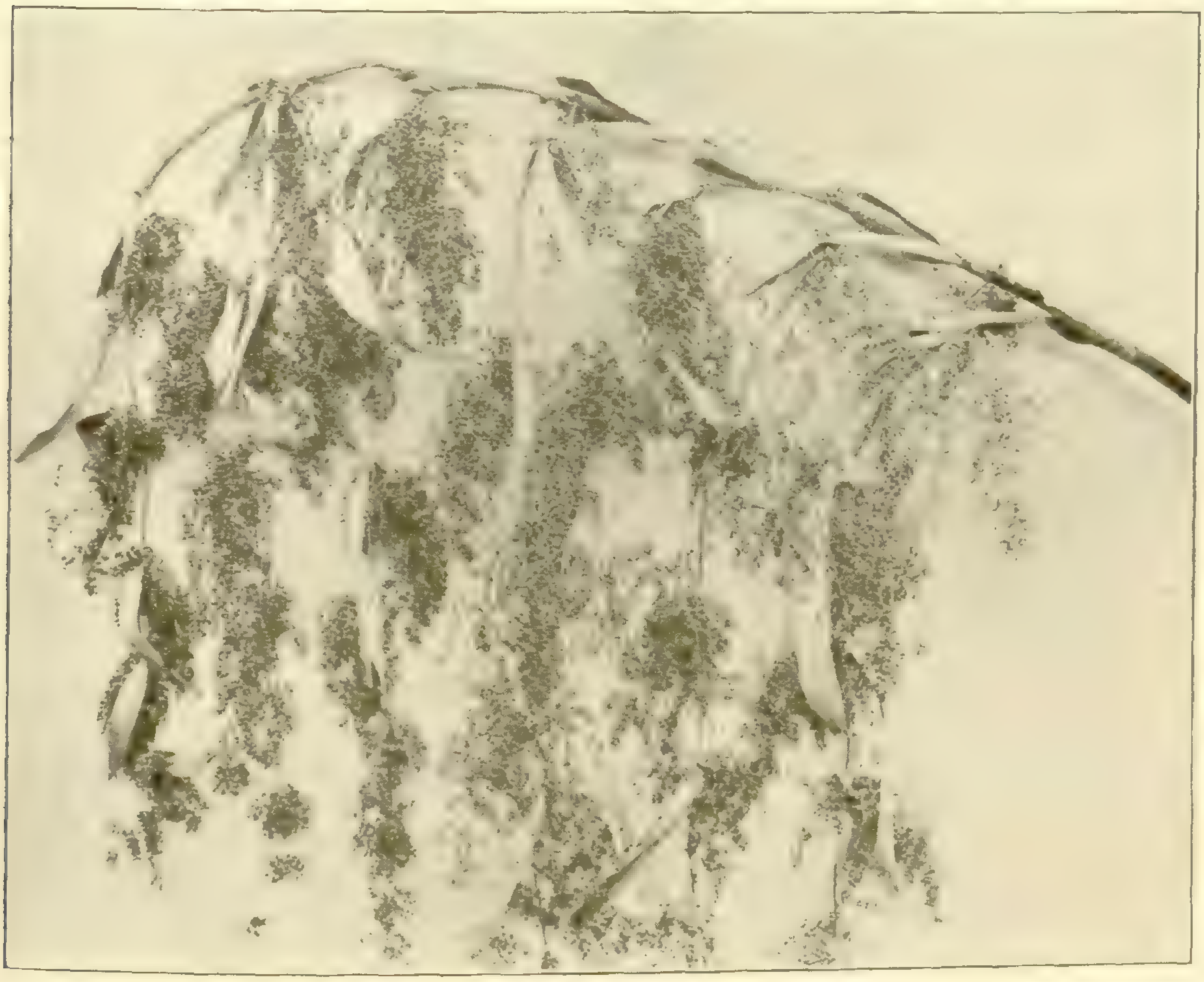

Fig. 10.—Panicle of *W. gracilis*, just setting fruit, from a tree on the lawn of Mr. D. W. McLeod, Arlington Avenue, Riverside, California.

ADDITIONAL NOTES ON W. FILIFERA ROBUSTA

Wendland's *Washingtonia robusta*, long considered an obscure if not, indeed, a mythical tree, is in reality the one with which we have the fullest acquaintance. The type source of *W. filifera* is unknown, the native home of *W. gracilis* remains unvisited, the haunts of *W. sonorae* seldom have been penetrated, but many botanists have stood beneath the groves of the desert *W. robusta*, and it has long been familiar in cultivation in southern California.

Distribution.—Its distribution appears to have been determined by the boundaries of the great lake which, in the not very distant past, occupied the central depression of the Colorado Desert. We may reasonably suppose the shores of this ancient lake to have been enlivened, here and there, with groves of stately palms. A few venerable trees still linger near the upper shore line of this vanished sea, gaunt and ready to perish, and without offspring to succeed them; but the most have retired to the cañons of the surrounding mountains. Here they find congenial homes along the few and feeble streams, by some scanty spring, or narrow oasis moistened by alkaline percolations. The necessity of soil moisture is the governing factor in their distribution.

The most extensive groves occupy a tract of strongly alkaline soil along the foothills some ten miles north of Indio, and extending up some of the neighboring washes. This belt may be considered the center of distribution. The finest grove occupies, for a mile or more, the narrow Palm Cañon, on the opposite side of the desert at the base of San Jacinto Mountain. Here hundreds of fine trees fill the sandy bed of the stream or cling to the rocky bases of its steep sides. The older trees are still vigorous, and there are abundant younger ones of all sizes. It is convenient of access from the little village of Palm Springs.

Most of the cañons at the desert bases of San Jacinto contain palms. A few grow in the cañon of the Whitewater, which is the western limit of the species. Its southern outpost is probably at Carrizo Creek; a few trees at Corn Springs mark its northern limit, and none are known east of Frink's Station.

Duration of the leaves.—It is seldom that one sees a desert palm, either indigenous or cultivated, that has not been marred by human agency. A naked trunk, crowned with living leaves, beneath which is a mass of dead ones deflexed, is not the natural aspect of the tree. The effete leaves, were they not artificially removed, would conceal

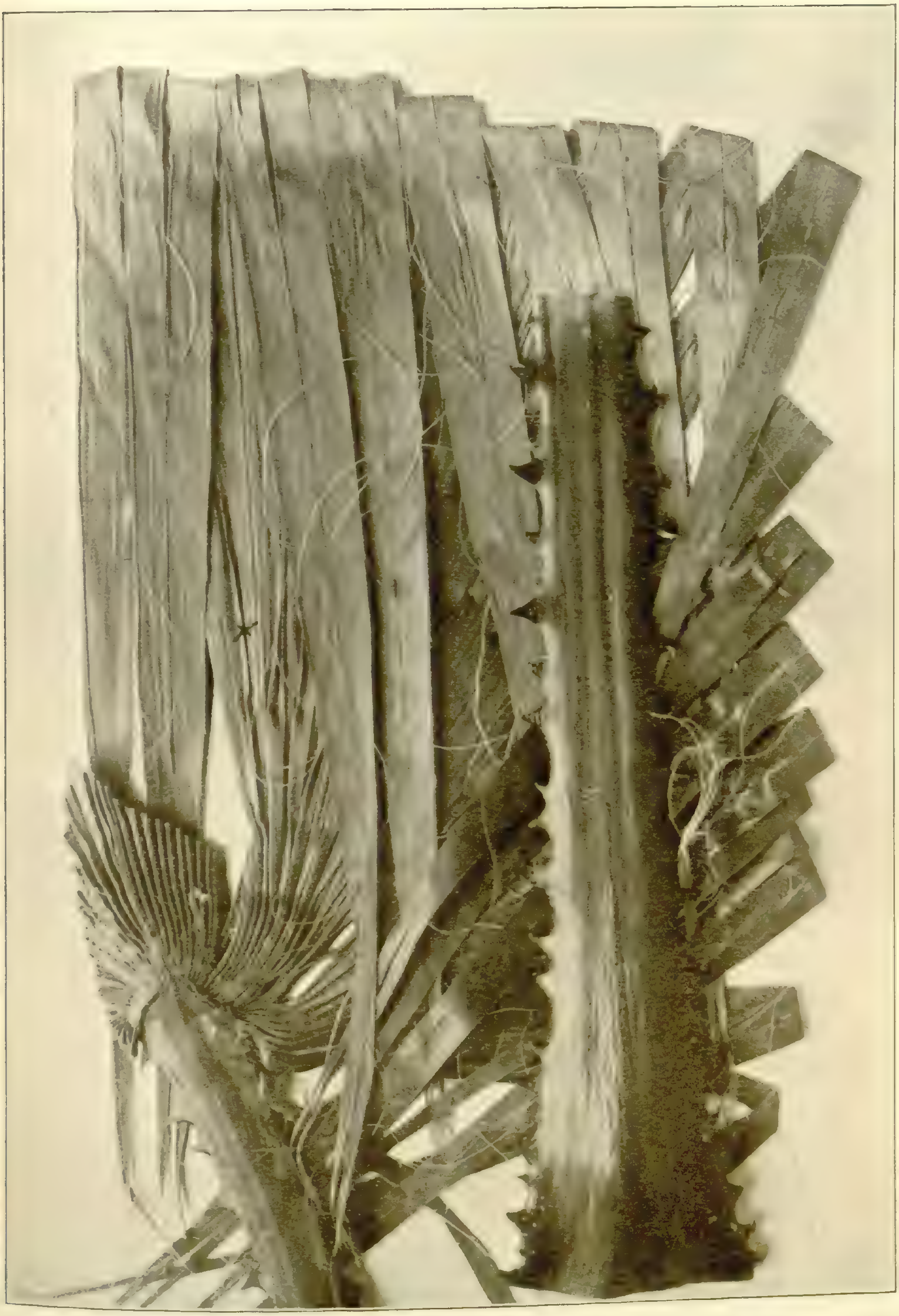

FIG. 11.—Leaf of *W. sonorae* S. Watson, from a tree in the Botanical Garden, Palermo, Italy.

the trunk, at least for the greater part of its length, beneath a gray thatch, an ideal protection against the parching air of the desert. The dead leaves are usually kept cut away from cultivated trees, while it is almost impossible to find mature indigenous palms from which the leaves have not been repeatedly burned. To so burn them was the immemorial custom of the desert Indians, and it has been erroneously alleged that in this they were influenced by a superstitious motive—the making of an offering by fire to the spirits of the dead. In fact their purpose was purely utilitarian, namely, to facilitate the gathering of the fruit, and, as they believed, to increase the fruitfulness of the trees. That the trees survive these repeated burnings is evidence of their wonderful vitality.

The functional life of a leaf is about one year. How long the dead leaves would remain attached to the trunk if undisturbed cannot be stated; probably for a very long period. There is a row of trees in San Bernardino fully 10^m tall from which the leaves have never been removed, and the lowest are over twenty-five years old and still firmly attached to the trunk. In a secluded nook of San Jacinto Mountain there is reported to be a group of three majestic palms, 20^m or more in height, whose trunks are clothed with a dense leaf-thatch from crown to base; their age cannot be less than a century. From the burned trees the leaves eventually fall off in great masses, the bases of the petioles seeming to have been violently wrenched loose, and not to have naturally separated, as with deciduous leaves.

Aboriginal uses.—The habitations of the desert Indians were mere shelters, but naturally palm leaves, when easily procured, were utilized in their primitive construction. Strands split from the leaves were convenient for tying, and it is said were sometimes used for the spiral coil with which they built up their baskets (MERRIAM :03).[11] They were also used in building the characteristic granaries used by these Indians for storing the various seeds used by them for food.

Of these food supplies the fruit of the palm was an important part. It was eaten fresh, and also dried for preservation. A favorite method of preparing the dried fruit was by triturating it with water

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[11] The stems of a grass, *Epicampes rigens*, was the material commonly used for this purpose. I have never seen a basket in the construction of which palm leaves had entered.

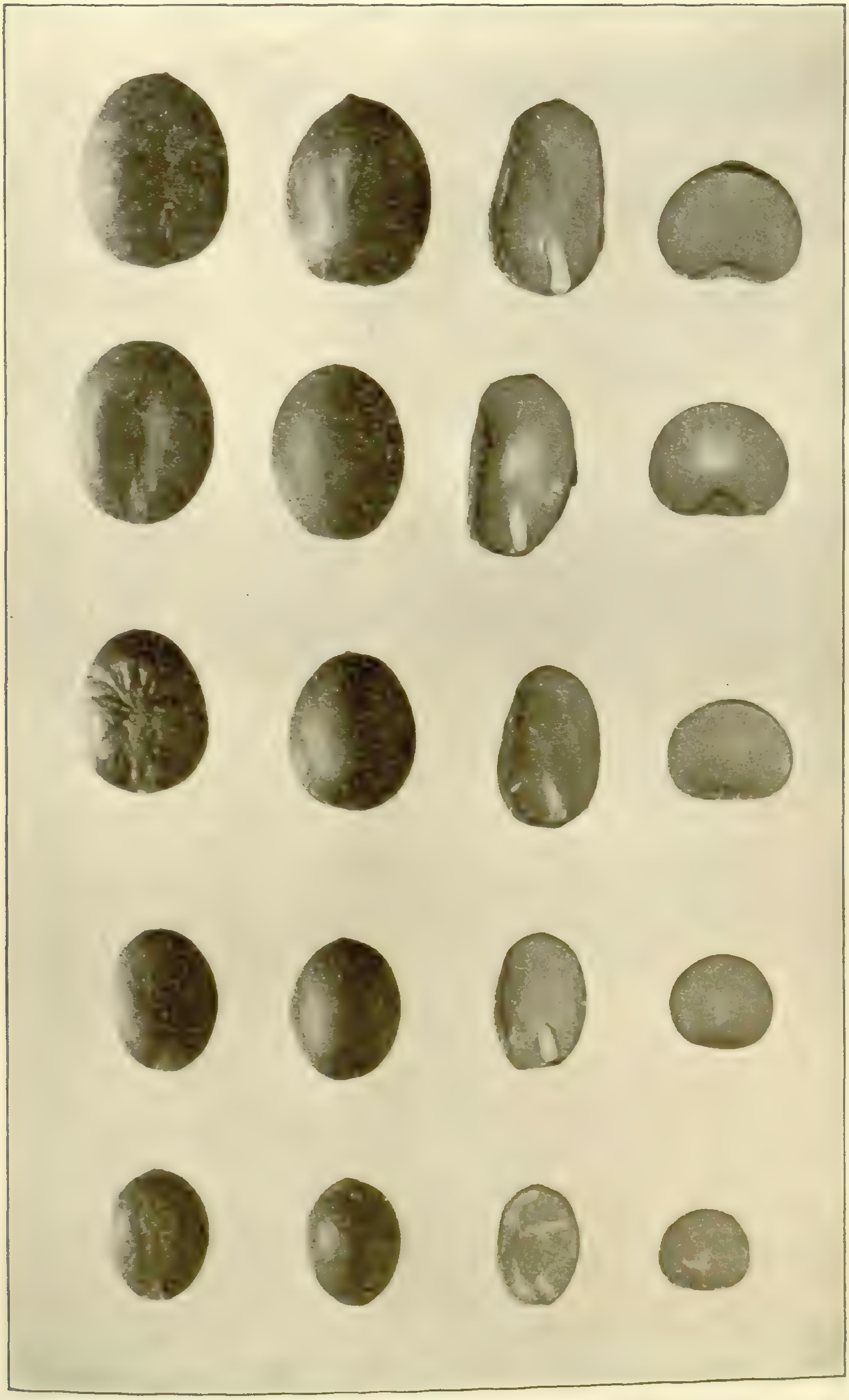

FIG. 12.—Seeds of Washingtonia; all ×3; *1* (bottom row), *W. filifera microsperma*, 4.8–5.8×3.5–4$^{\text{mm}}$; *2*, *W. filifera*, 5.8–6×4–4.5$^{\text{mm}}$; *3*, *W. gracilis*, 6–7×4.8–5.3$^{\text{mm}}$; *4*, *W. filifera robusta*, 7–8×5.5–6$^{\text{mm}}$; *5*, *W. sonorae*, 7–8.5×5.5–6.5$^{\text{mm}}$.

in a stone mortar until a pulpy mass, rich in saccharine properties, was produced. The seeds were then separated and the pulp was thickened with meal made from pounded "chia" (Salvia), or grass seed, or pine nuts. The bony seed itself was pounded into meal, which Dr. EDWARD PALMER ('78), who seems to have tried it, pronounces "not inferior to cocoanut," a statement which may be accepted with some reservation. The terminal bud also was baked and eaten. The Coahuilla name of the palm is *Mau-wal*. Each grove was the property of a particular clan, to whom alone belonged the right to gather the fruit.

An insect enemy.—The desert palm is not known to be infested by any parasitic fungus, or to be subject to any bacterial infection. Its sole enemy is the larva of a Bostrychide beetle, *Dinapate Wrightii* Horn, the only species of the genus. The female oviposits at the base of the living leaves, whence the larva bores downward through the trunk, its continually enlarging galleries becoming at length 18^{mm} in diameter. These are tightly packed, for the most part, with rejected gnawings. The larval life of the insect is three or four years, perhaps even longer. The mature beetle has a length of fully 5^{cm} and is the heaviest North American coleopter.

The number of contemporaneous larvae that may inhabit a single trunk has been estimated as high as 200 or 300; but Mr. W. G. WRIGHT, who discovered the beetle, and who has assiduously investigated its habits, is of opinion that it would probably not exceed 50. But even such a horde of huge and voracious grubs, in their comparatively long life, might riddle a whole trunk with their galleries. They seem not to work any great destruction to the groves, however; in fact, the only evidences of their presence to the ordinary observer are the exit holes in dead trunks.

ACKNOWLEDGMENTS

In the preparation of this account I have been greatly aided by information communicated by several friends. I especially desire to record my thanks to Dr. ODOARDO BECCARI, the distinguished palmographer of Florence, Italy, for valuable notes regarding the Washingtonias cultivated in Europe, and for the photographs illustrating them. Other photographs were kindly made for me by Mr.

W. G. WRIGHT. For copies or abstracts of papers not otherwise accessible to me I am under obligations to Mr. H. M. HALL, of the University of California, Miss MARY A. DAY, librarian of the Gray Herbarium, Dr. J. N. ROSE, of the National Herbarium, and Mr. C. E. FAXON, of the Arnold Arboretum. Dr. WELWOOD MURRAY, for many years a resident of Palm Springs, has favored me with some notes on the use of the palm by the Indians.

SAN BERNARDINO
CALIFORNIA

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ARAUCARIOPITYS, A NEW GENUS OF ARAUCARIANS[1]

EDWARD C. JEFFREY

(WITH PLATES XXVIII–XXX)

Among the coniferous remains discovered in the Cretaceous deposits of the Androvette pit, Kreischerville, Staten Island, are certain leafless twigs, bearing spirally arranged scars. In most cases the twigs in question are decorticated as well as deprived of their appendages; in fact, in all the best-preserved material this is the case. An examination of the internal structure of these remains showed that they were Araucarian in their affinities; but possessed deciduous shoots, similar to those occurring in Pinus. The deciduous shoots seem to have been of seasonal duration only. The branches of the type described above were found in association with impressions of the deciduous leaf-fascicles of Czekanowskia, a supposed but doubtful representative of the Ginkgoales. It is not improbable that the two sorts of remains belong to each other, although it is impossible to more than infer that such is the case at the present time.

Fig. 1 represents a transverse section through a rather well-preserved stem of our species, which we propose to call **Araucariopitys americana,** for reasons to be stated later. The lower right-hand portion of the section is in a bad state of preservation. There are two marked indentations of the surface of the decorticated stem; these mark the positions of two deciduous leafy shoots. The indentation on the extreme right of the figure occurs in the less well-preserved region, so that the topography of the relation of the deciduous shoot to the supporting axis is not clear. The indentation on the upper left-hand part of the surface of the stem corresponds to a short shoot, which is not cut axially by the plane of section. In the well-preserved part of the wood it is obvious that there is but a single annual ring present. A noteworthy feature of the wood is the presence of a tangential row of traumatic resin canals. These traumatic canals are very common in this species, occurring in nearly half the specimens in our possession. It would thus appear that the species was very easily stimulated to the formation of traumatic resin ducts.

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 11.

The pith is not well shown in *fig. 1* on account of the partial decay of the specimen. In *fig. 3* it appears more clearly, and it is possible to distinguish that there are certain dark areas in it, which correspond to islands or nests of sclerotic cells, similar to those which are found in the medulla of the Cretaceous genus Brachyphyllum. The pith is relatively large in size, exceeding in its proportions that found in living Cupressineae. *Fig. 3*, which was made from a section higher up in the branch than that which supplied *fig. 1*, shows on the upper right-hand side the presence of a small portion of the cortex and bark *in situ*. In the cortex are present, although this feature is not apparent in the figure, the same islands or nests of sclerotic tissue which are found in the medulla.

Fig. 2 shows the cross-section of another less well-preserved stem, which has lost part of its woody tissues, but still retains a considerable portion of its bark. The apparent cracks in the wood represent rows of resin canals, which the magnification is not sufficient to make apparent. *Fig. 4* illustrates a part of the same stem as that shown in *figs. 1* and *3*, under a higher magnification. The row of traumatic resin canals can be particularly well made out here and also the sclerifications, which appear as dark spots in the pith.

Fig. 5 shows a portion of the section figured in *fig. 1*, under a considerable degree of magnification. The absence of resiniferous cells, such as are a feature of the wood of the Cupressineae, can be made out. A number of rounded cavities appear in the wood, which are the traumatic resin canals. By their rounded contour, they more nearly resemble those of the Abietineae in aspect than those of any other of the Cretaceous Araucarineae which we have studied. The resin canals are surrounded by one or more layers of parenchyma cells, which appear to be devoid of contents. Often there is present in the lumen of the canals themselves a dark-hued substance, which is in all probability a fossil gum or mucilage, since it is not soluble in any of the numerous solvents of resin used hot in the process of preparing the material for sectioning. This substance apparently corresponds to that described as present in the traumatic resin canals of other Araucarian lignites from various levels of the Cretaceous.[2]

Fig. 6 shows a tangential longitudinal section of the wood of our species, through the region of the traumatic resin canals. It is to be noted that these are more numerous than is the case with normal resin canals, and are somewhat constricted at intervals, both features to be found in the wound-canals of the Abietineae. In the region of disturbance shown in *fig. 6*, the rays vary greatly in height, being composed of from one to many cells. *Fig. 7* shows the left-hand portion of *fig. 6*, more highly magnified. In this figure the end walls of the ray cells, which appear in face view, are strongly pitted, a feature found in no other living or fossil Araucarian, which has been described, but very characteristic of the Abietineae. Both the end and horizontal walls of the ray cells in Agathis and Araucaria, for example, are smooth, and this statement equally holds for the numerous species of Mesozoic Araucarians which it has been possible to study in the Androvette deposits. Our present species differs, then, from all other Araucarians, living or extinct, in the presence of abundant pitting on the terminal and horizontal walls of the cells of its medullary rays. The cells constituting the rays are entirely parenchymatous and there are no tracheidal cells present, such as occur in the rays of certain species of living Abietineae. *Fig. 9* shows with sufficient clearness the strongly pitted horizontal wall of the ray cells in our species.

In *fig. 8* is seen a longitudinal approximately radial section of the wood in Araucariopitys. The magnification is scarcely sufficient to show the araucarian radial pitting of the tracheids. This section shows very well, however, the constriction of the traumatic resin canals at intervals, which Professor PENHALLOW, in the case of the traumatic and normal resin canals of certain Abietineae, has interpreted as an indication of the derivation of the continuous system of resin canals, present, for example, in Pinus, from the union with each other of a number of originally isolated resin spaces or cysts.[3] This view, as will be shown on another occasion, can scarcely be accepted.

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[2] JEFFREY, E. C., The wound-reactions of Brachyphyllum. Annals of Botany **20**:383–394. *pls. 27, 28.* 1906.

[3] PENHALLOW, D. P., The anatomy of the Coniferales. Amer. Nat. **38**:243 ff. 1904.

Fig. 10 shows the structure of the pith in our species. It will be seen that it is traversed at intervals by diaphragms of sclerenchymatous cells, which strongly recall those to be found in Abies, Picea, and certain hard pines. The stone cells are arranged in longitudinal rows, as if they had been formed by the transverse divisions of a horizontal series of mother cells, as has been described in certain Calamites and Equiseta. *Fig. 11* illustrates the character of the radial pitting in our species. It will be seen by examination of the pits on the left of the figure that some of them are in intimate contact and are mutually flattened, in the manner characteristic of the radial pitting of *Araucarioxylon* Kraus. There is a clear distinction from the typical condition in Araucarioxylon, however, in the fact that not all the pits are mutually flattened, but some of them are rounded in contour, as in the wood of the Abietineae. The pitting in our species is thus transitional between the types characteristic of Araucarioxylon and Pityoxylon or Cedroxylon. In the general memoir on the Conifers of the Androvette Cretaceous deposits, it has been proposed that woods of a type transitional between the modes of radial pitting found in the Araucarineae and Abietineae should come under a new genus Brachyoxylon, taking the wood of the genus Brachyphyllum as the type. Our present species, however, can scarcely be put under Brachyoxylon, since in the latter the terminal and horizontal walls of the ray cells are smooth as in the living Agathis and Araucaria and their near allies of the Mesozoic. In the species under discussion, by contrast the terminal and horizontal walls of the ray cells are both strongly pitted, as is typically the case in the Abietineae. If other species of lignites are subsequently discovered which agree with that under discussion in their essential features, it will probably be well to establish the name Araucariopityoxylon or some convenient abbreviation of it for their reception. So long as the type is represented by a single lignitic species, however, the name Araucariopitys will suffice both for the branches and the wood. On the other hand, if it is proved subsequently that Araucariopitys represents the branches of Czekanowskia, as we strongly suspect to be the case, both names will have to be merged in Czekanowskia.

In *fig. 12* is shown a highly magnified view of the radial pitting of the species under discussion. The field is so chosen as to include mainly tracheids, showing the araucarian type of pitting. Occasionally a tracheid may be found in longitudinal sections of our species, broad enough in its terminal region to accomodate a double row of pits, in which case the phenomenon of alternation as well as flattening may be observed, although even the biseriate pits are sometimes found to be opposite as in the Abietineae. It may be questioned by the reader whether the evidence afforded by the pitting alone is strong enough to decide the Araucarian affinities of the genus we have been describing. We have no inclination to deny the propriety of such a doubt, but we consider it to be removed by the fact that the large number of presumably transitional Araucarians found in the form of well-preserved leafy branches in the Androvette deposits were accompanied by numerous associated cone-scales, which, where they did not obviously belong to Pinus, were also Araucarian and of a transitional type of organization. For a full discussion of this matter the reader is referred to the joint memoir already cited.

Fig. 13 illustrates the short shoot of Araucariopitys as seen in tangential section under low magnification. The brachyblast is present in the upper part of the field. Below it there is a scarcely perceptible disturbance in the arrangement of the tracheids, indicating the position of the foliar trace, to which the short shoot is axillary. It is apparent, from the topography of the tangential section of the wood, that the axillating leaf was better developed in Araucariopitys than is generally the case in Pinus, where the subtending foliar organ is usually obsolete or has degenerated into a mere scale. There are of course in Pinus certain exceptions to this statement in the case of seedlings and the shoots growing out of injured branches. In *fig. 14* is represented a more highly magnified view of the section of the same short shoot shown in *fig. 13*. *Fig. 15* represents a radial section through the axis of the short shoot, which at the same time includes a part of the woody cylinder and the pith of the parent axis. In *fig. 16* is seen a transverse section through the main axis at the level of exit of one of the brachyblasts. It is easy to determine from the sections just described that the woody cylinder of the short shoot projects little if at all beyond the surface of the wood of the main axis. *Figs. 12–17* have all been made from another specimen than that which furnished *figs. 1, 3, 4, 5*. *Fig. 17* presents a somewhat magnified image of the transverse section of the axillating leaf trace as seen in longitudinal section of the axis. There is obviously a considerable disturbance in the arrangement of the tracheids of the axis.

All the available specimens of our fossil showing the bark in place are unfortunately badly preserved. They confirm the conclusion, however, that Araucariopitys possessed deciduous shoots comparable with those of living pines and at the same time was an araucarian Conifer. The condition of preservation in the corticated specimens makes it possible to observe that the deciduous shoots have already fallen in branches which show but a single annual ring and are subtended by definite absciss layers occurring in the outer cortex. There are no peridermoid tissues present except in the limited areas immediately opposite the deciduous shoots.

It will be obvious to the reader that in the coniferous branches to which we have assigned the name Araucariopitys, there are features present which combine in a remarkable degree the anatomical characteristics of both the Abietineae and Araucarineae. The radial pitting of the tracheids, for example, as has been shown above, is clearly transitional between the two orders. The rays tend more strongly to the abietineous side. The wound-reactions of our Conifer are more like those of the Abietineae than are those of any other known Araucarian. Finally, the genus was characterized by the possession of deciduous shoots. It will be obvious from the enumeration of the features that in the species under discussion we have a strong araucarian endowment with a nearer approach to abietineous structure than has been found in any Araucarian living or extinct. Since this is the case, the name Araucariopitys, etymologically significant of the double affinities, seems appropriate.

CONCLUSIONS

It appears from the description given above that there are present in the Cretaceous deposits of Kreischerville, Staten Island, N. Y., certain branches with deciduous lateral shoots, resembling in their relation to the axis the brachyblasts in the abietineous genus Pinus. Further, it is apparent that in spite of the possession of deciduous shoots, the branches in question belong to an araucaraian Conifer of archaic type, as is shown by their anatomical structure. The wood of these shoots presented the wound-reactions of the Abietineae, radial pitting of the tracheids transitional between the Abietineae and Araucarineae, and the ray structure of the Abietineae. It is moreover probable that leafy shoots known under the generic appellation of Czekanowskia belonged to our species, since the former occur in impressions in association with these remains.

It appears clear that in Araucariopitys we have to do with a genus transitional in its characters to a marked degree and nearer to the Abietineae than any other known araucarian genus living or extinct. The existence in the Mesozoic of types like Araucariopitys, Brachyphyllum, Geinitzia, etc., combining in so many ways abietineous and araucarian characters, does not make it easy to accept as correct the position recently adopted by Professor SEWARD[4] that the Araucarineae are distinct from, and without immediate affiliations with, the other coniferous orders. It is indeed not difficult to show that the aberrant forms which represent the Araucarineae in the existent flora are sufficiently different from the Abietineae and most of the other coniferous families; but such a conclusion cannot now be projected into the past, in the face of our recent fuller knowledge of the structural features of the araucarian flora of the Mesozoic.

Since it must apparently be admitted that in the Mesozoic the abietineous and araucarian Conifers were not so clearly separated from each other as the living representatives of those families are, the question arises, which of these two admittedly ancient families lies nearer to the ancestral stock? Professor SEWARD and others have argued, from the rich luxuriance of the araucarian flora in the Cretaceous and even earlier periods of the Mesozoic (a luxuriance which our own studies, as described in the monograph already referred to, only serve to emphasize), as compared with the comparative poverty of the abietineous display, for the superior antiquity of the araucarian Conifers. Such an argument appears, however, to be fallacious. It would be just as logical to assume that at any given period the richly developed crown of a forest tree was its oldest portion. All the evidence goes to show that the Araucarians were indeed the crown of the coniferous genealogical tree during the Mesozoic, but in the changes which ushered in the Tertiary the crown was almost completely destroyed and that a lower more ancient and overshadowded branch, the Abietineae, became a new "leader" and developed luxuriantly.

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[4] SEWARD, A. C., and FORD, S. O., The Araucarieae, recent and extinct. Phil. Trans. Roy. Soc. London B. **198**:305–411. *pls. 23, 24.* 1906.

Concerning the derivation of the Araucarineae from the Abietineae in the beginning of the Mesozoic period, evidence has rapidly accumulated of late. Reference has been made above to the striking abietineous characteristics of the older Araucarians. It has been pointed out that the wound-reactions of the older Araucarineae are a strong indication of their abietineous derivation. Further, although the older Araucarians show striking transitions in their pitting toward the Abietineae, even the most archaic structurally known abietineous type, Prepinus, shows no tendency whatever toward the araucarian form of bordered pit. In the case of Prepinus just referred to, we are moreover forced to the conclusion that we have to do with an extremely ancient coniferous type, since the foliar bundles show an abundant development of true centripetal wood as distinguished from mere transfusion tissue. Further, the leaf traces are completely surrounded by a complicated double sheath of transfusion tissue, which has its exact counterpart in certain Cordaites but not elsewhere. Prepinus, in other words, manifests a nearer affinity to the ancestral Gymnosperms than any other known Conifer, and at the same time is clearly related to the Cretaceous species of Pinus, as is shown in the article cited. An additional argument for the superior antiquity of the Abietineae is afforded by the morphology of the female cone. It is true that Professor SEWARD, in the memoir cited above, has questioned whether the same morphological explanation can be offered of the female cone in the Abietineae and Araucarineae, in view of what he considers to be the slight degree of relationship between them. That the two families must be regarded as somewhat nearly allied we have tried to show above. If it be admitted that they are closely connected it follows that a common explanation of their ovulate strobilus should be possible. If we accept the generally approved explanation of the double cone-scale present in the female cone of the Abietineae, namely, that the upper ovuliferous scale is an axillary structure of shoot value subtending the sterile bract, then we are almost driven to regard the single cone-scale of the Araucarineae with its *double* system of bundles as having resulted from the *fusion* of the two organs present in the Abietineae. If this be granted, it is not easy to deny to the Abietineae a superior antiquity.

SUMMARY

1. Araucariopitys is an araucarian Conifer found in the Middle Cretaceous Clays of Staten Island, N. Y.

2. Its structure and its association with impressions of the leaf-fascicles of Czekanowskia make it possible that it constitutes the branches of that genus, which in such a case cannot be regarded as belonging to the Ginkgoales.

3. Araucariopitys was characterized by the possession of deciduous shoots, which apparently persisted for a single year; by the characteristic radial pitting of its tracheids, transitional between true araucarian pitting and that found in the Abietineae; by rays differing from the araucarian type and approximating the abietineous type; by the formation of traumatic resin canals closely resembling those found in the Abietineae.

4. Araucariopitys, although unquestionably araucarian, was nearer in structure to the Abietineae than any other known araucarian genus living or extinct, and has been named in accordance with this fact.

5. Araucariopitys supplies additional evidence for the derivation of the Araucarineae from the Abietineae.

Phanerogamic Laboratories
Harvard University

EXPLANATION OF PLATES XXVIII–XXX

PLATE XXVIII

Fig. 1. Transverse section of stem of *Araucariopitys americana.* ×30.

Fig. 2. Transverse section of another specimen of the same. ×18.

Fig. 3. Transverse section of stem of *Araucariopitys americana* from the same specimen as *fig. 1.* ×24.

Fig. 4. Transverse section of part of the same. ×40.

Fig. 5. Transverse section of the same to show the traumatic resin canals. ×180.

PLATE XXIX

Fig. 6. Tangential longitudinal section of *Araucariopitys americana.* ×100.

Fig. 7. Tangential section of the same. ×180.

Fig. 8. Longitudinal approximately radial section of the same. ×40.

FIG. 9. Radial section of the same, showing structure of the ray. ×500.

FIG. 10. Section of the medulla of the same. ×40.

FIG. 11. Longitudinal radial section of the same. ×180.

PLATE XXX

FIG. 12. Longitudinal section of the tracheids of the same to show Araucarioxylon pitting. ×500.

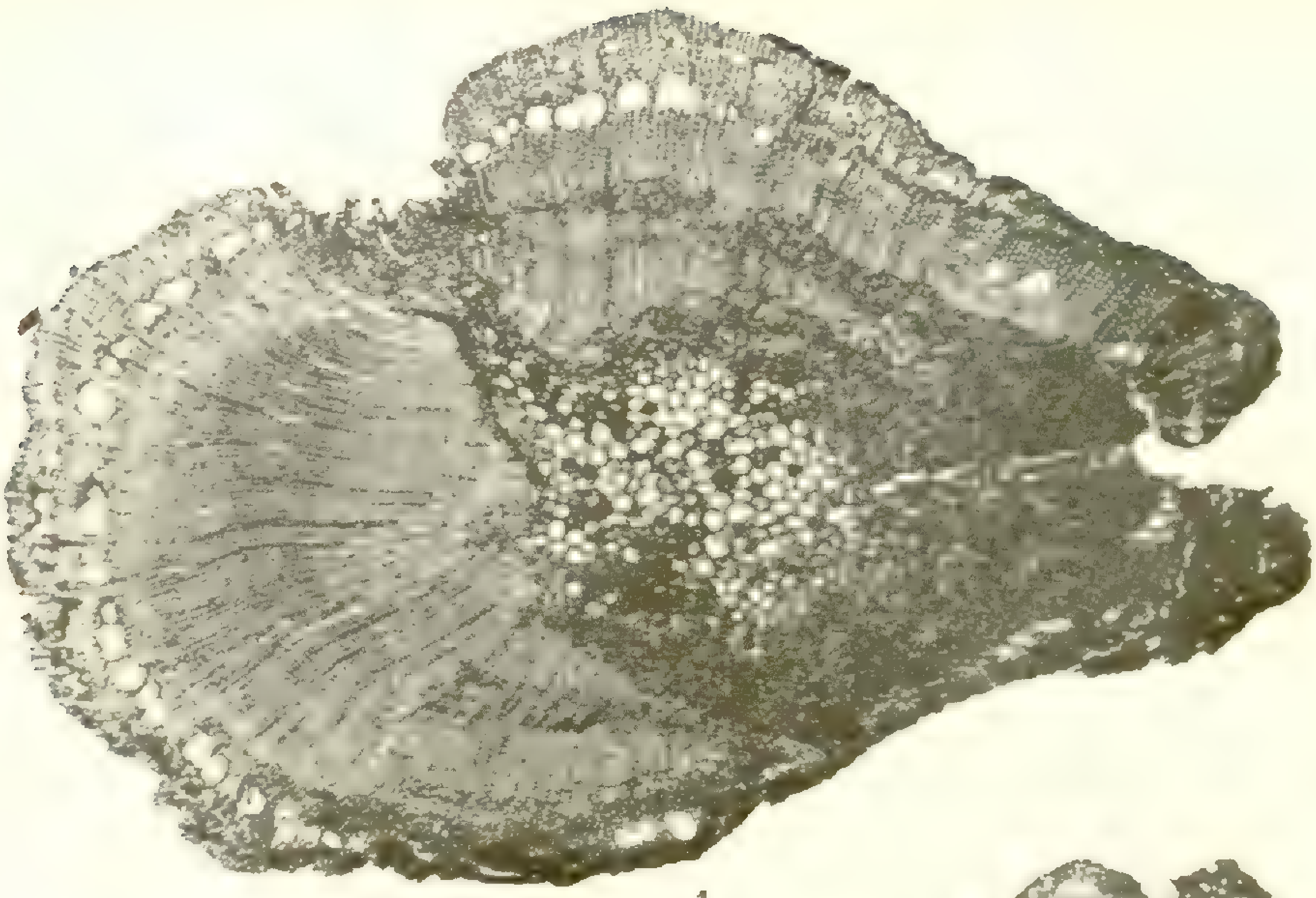
FIG. 13. Tangential section of main axis of Araucariopitys, showing the presence of a short shoot and its axillating leaf trace. ×25.

FIG. 14. The short shoot of the same. ×40.

FIG. 15. Radial section through the deciduous shoot of the same. ×40.

FIG. 16. Transverse section of wood of Araucariopitys, showing the base of the deciduous shoot in longitudinal section. ×40.

FIG. 17. Tangential section of wood of Araucariopitys, showing the trace of the axillating leaf in transverse section.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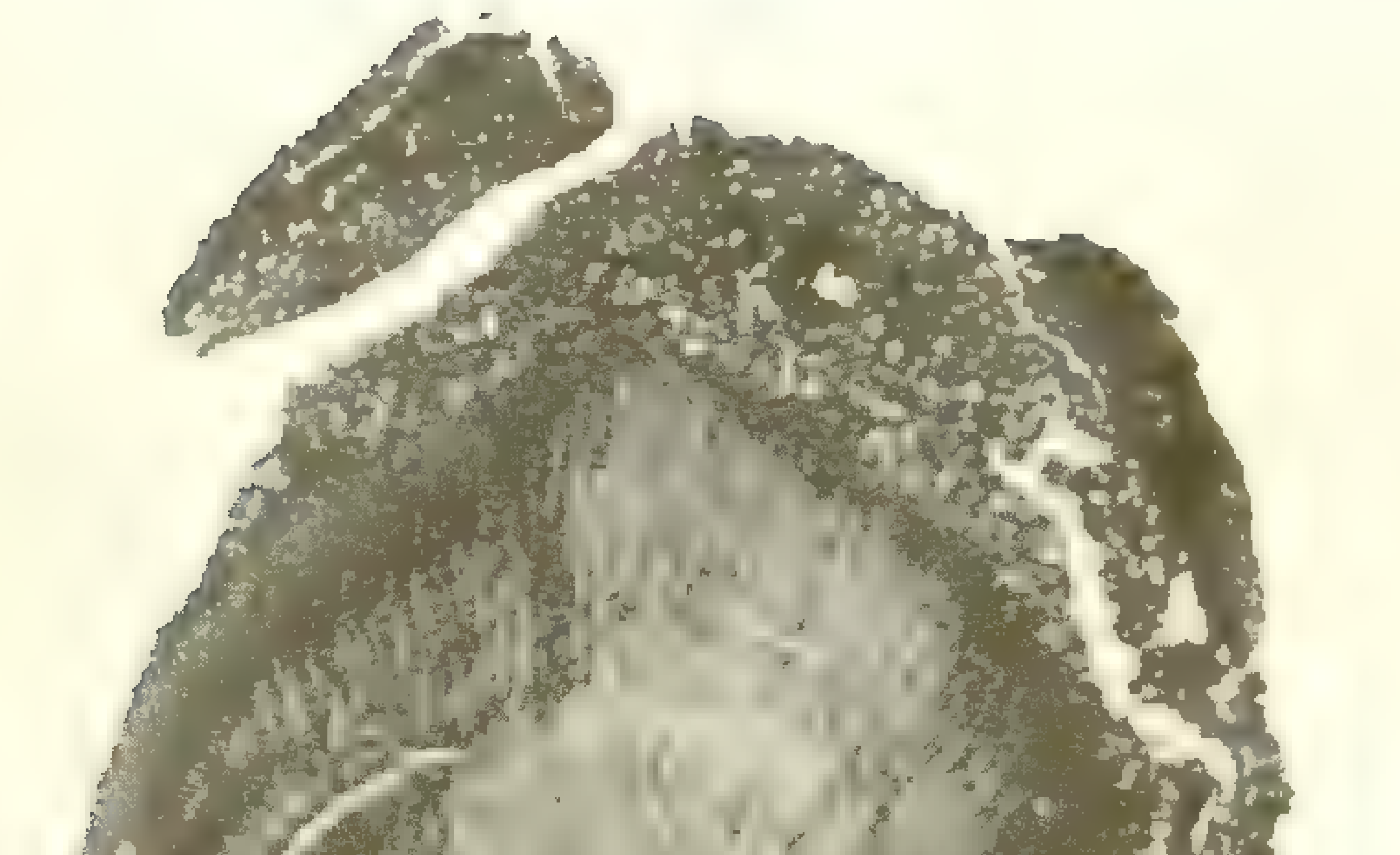
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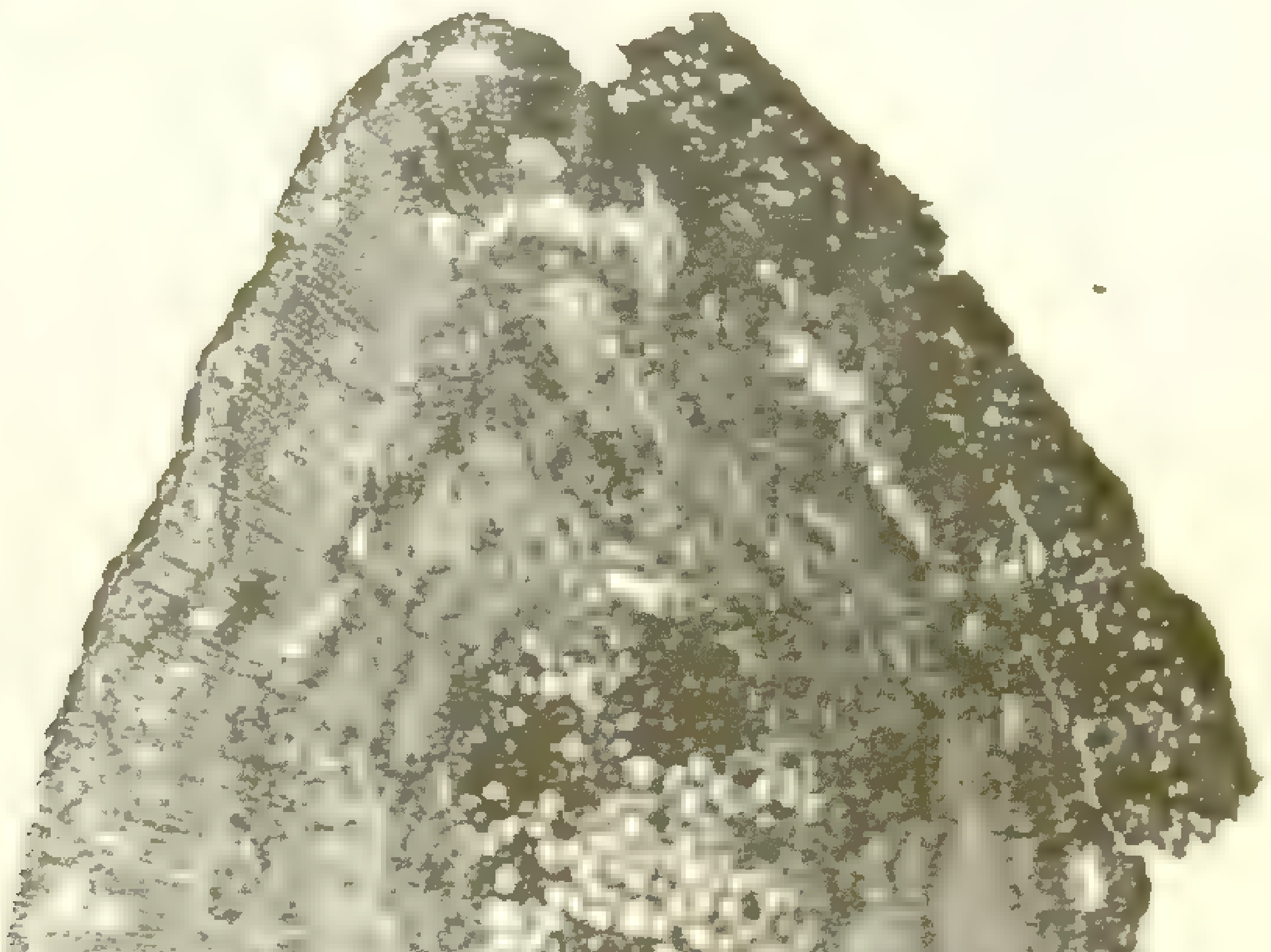
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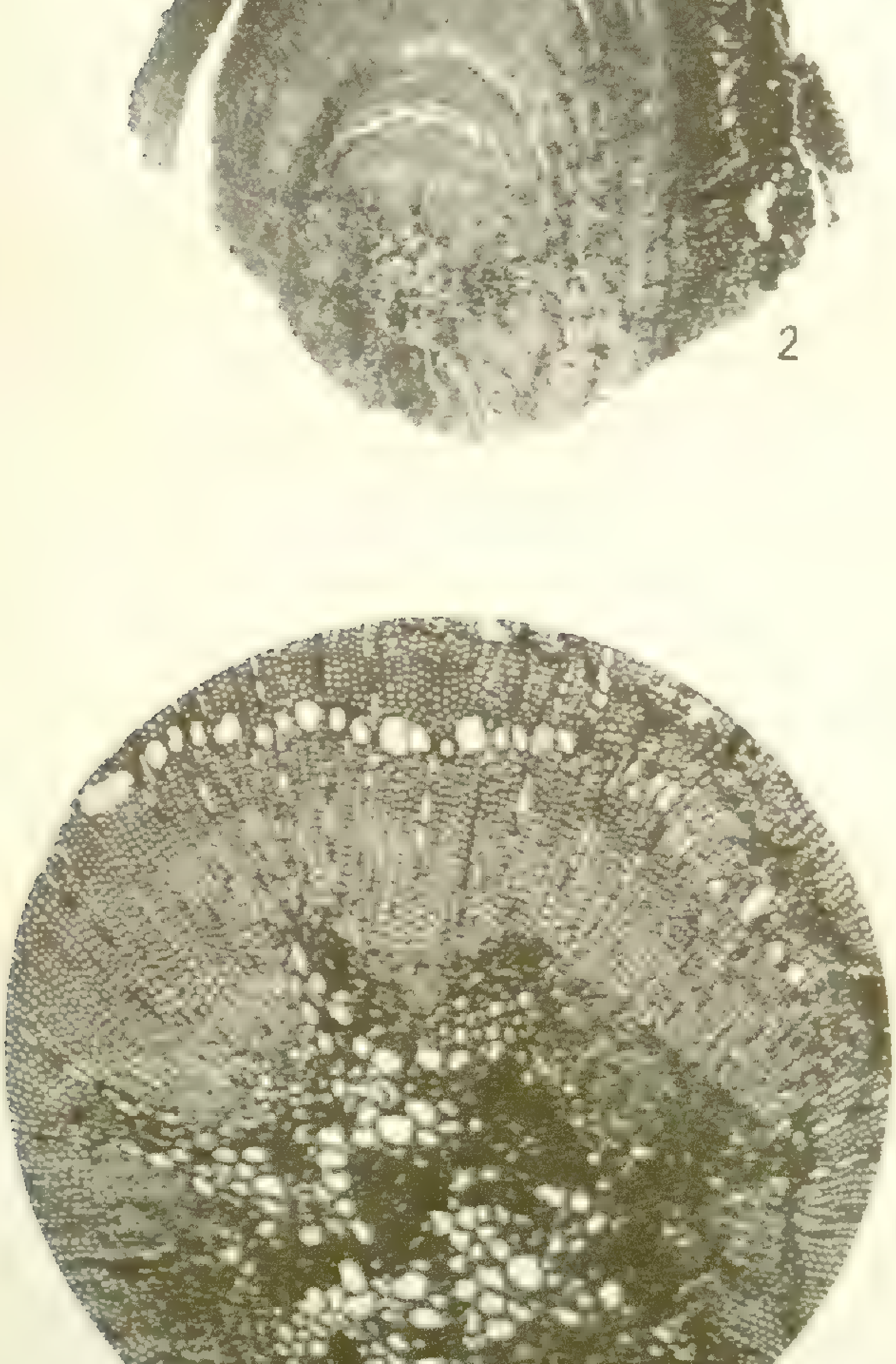
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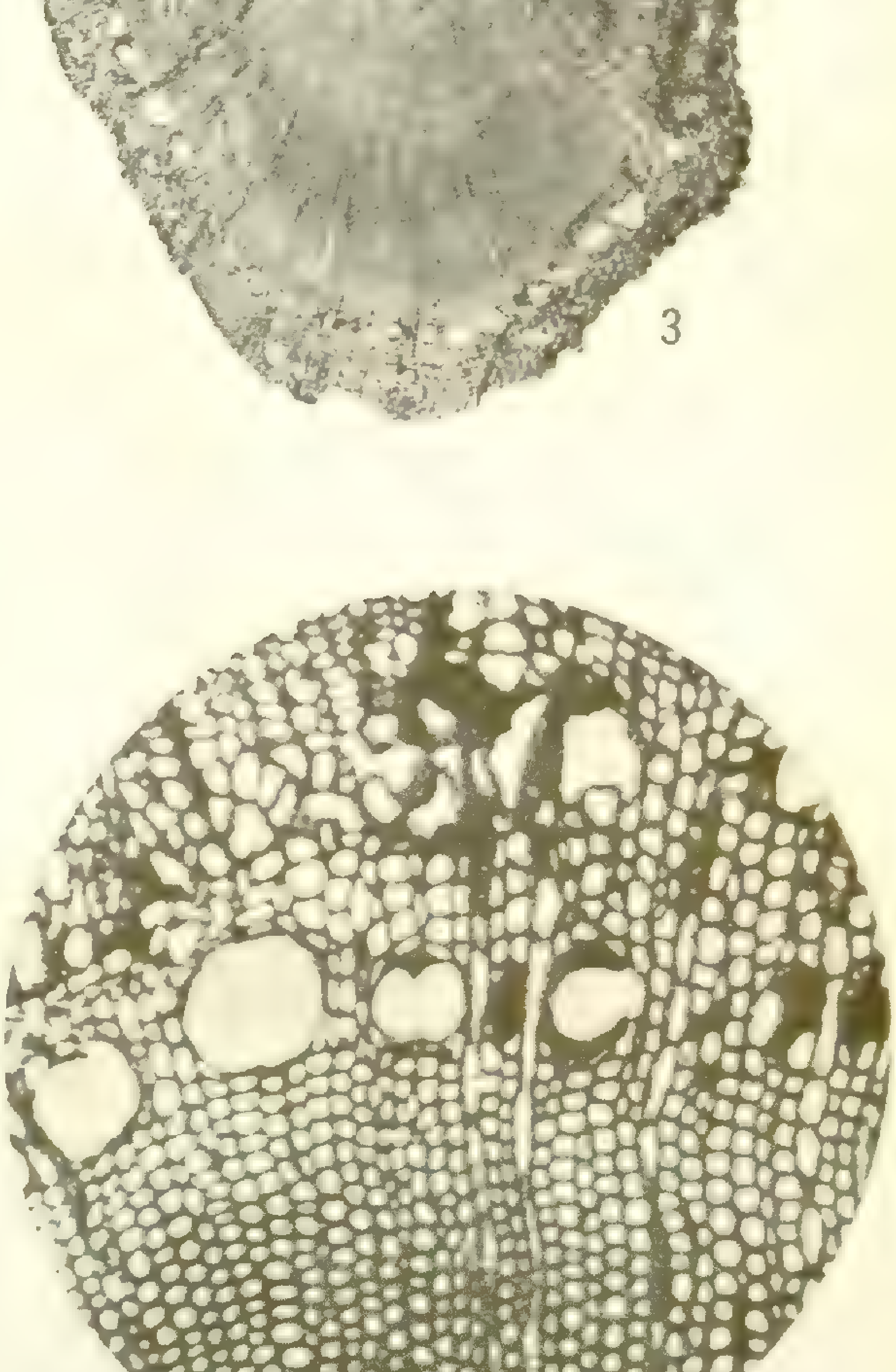
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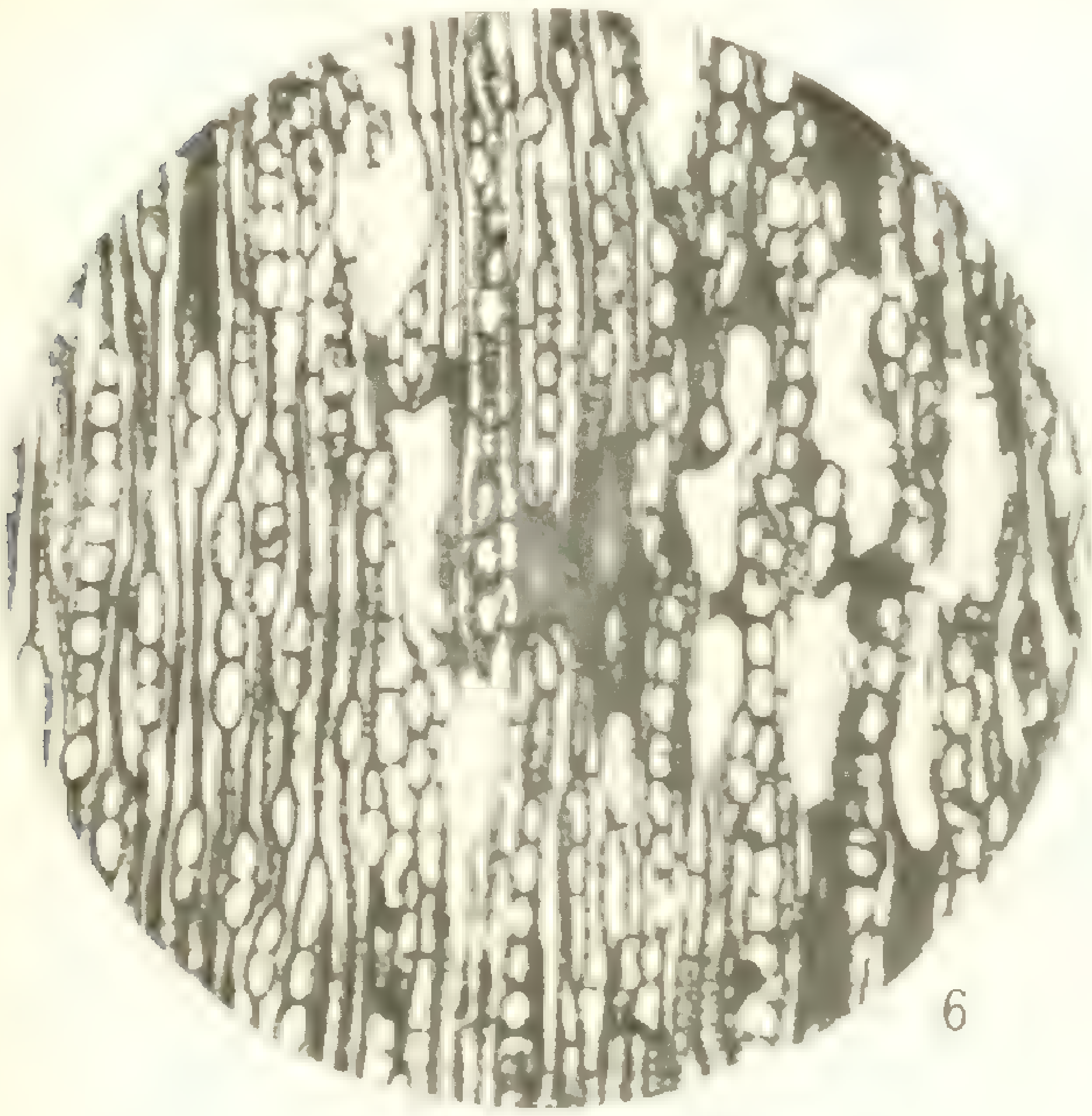
JEFFREY on ARAUCARIOPITYS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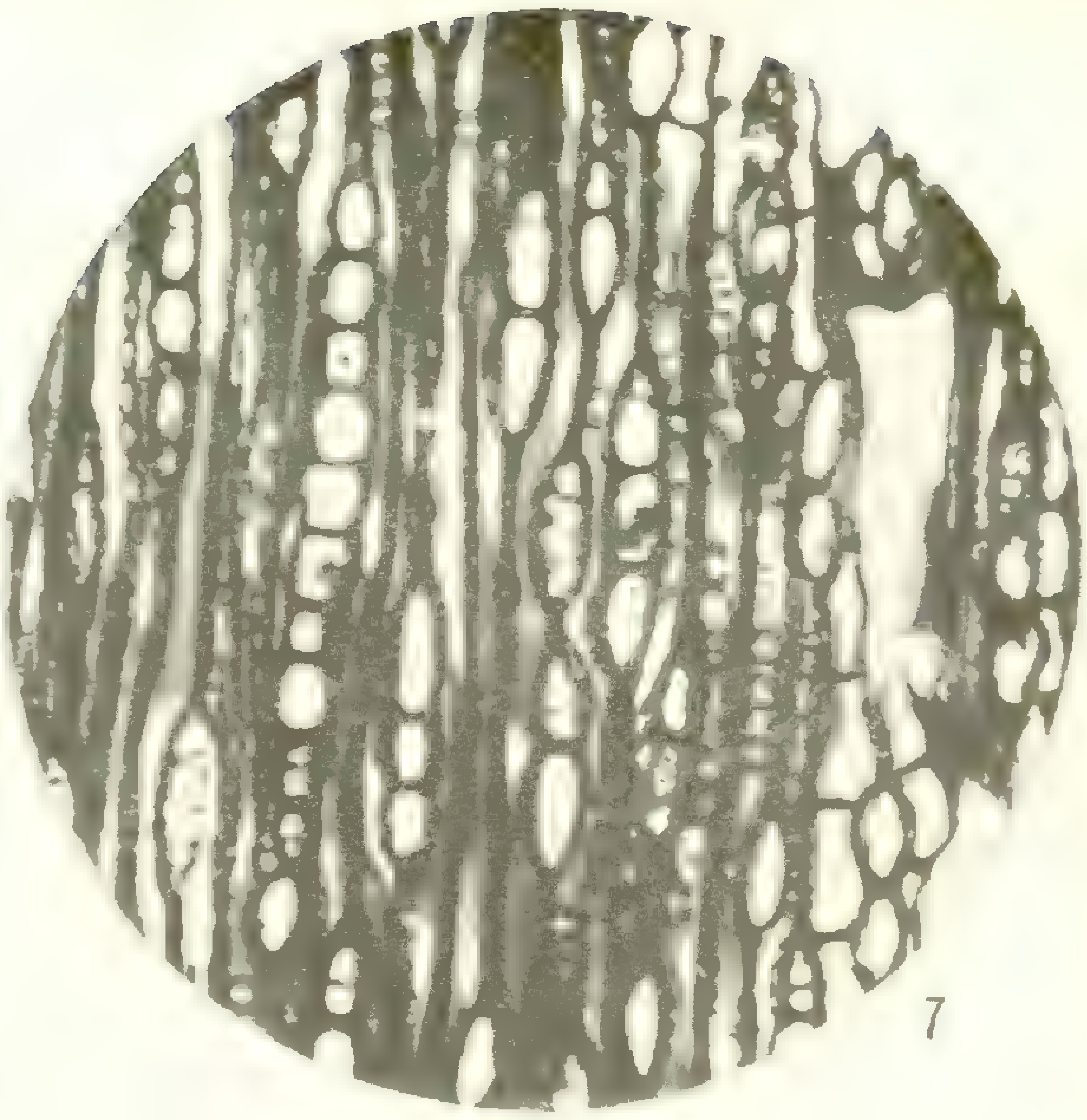
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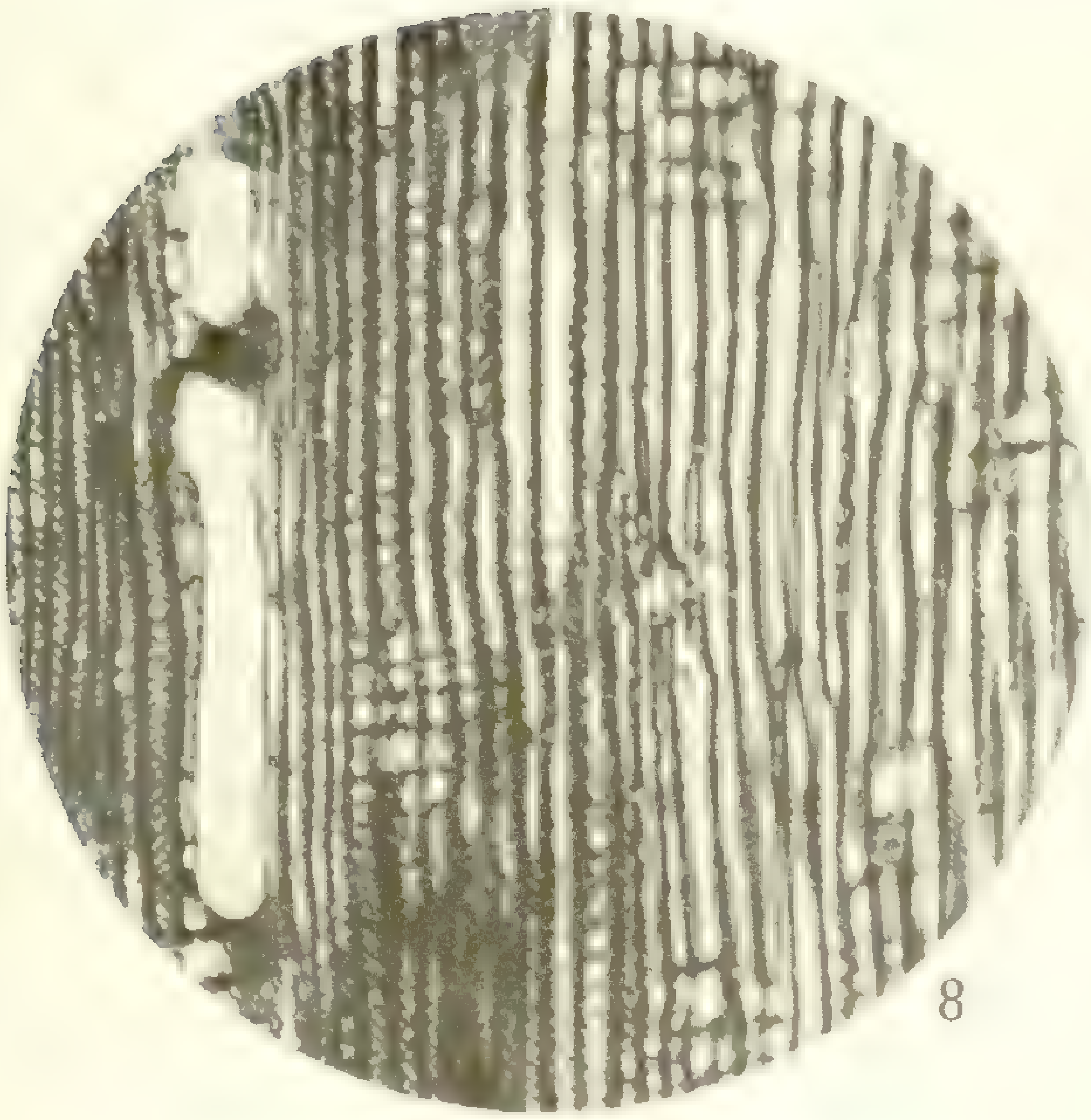
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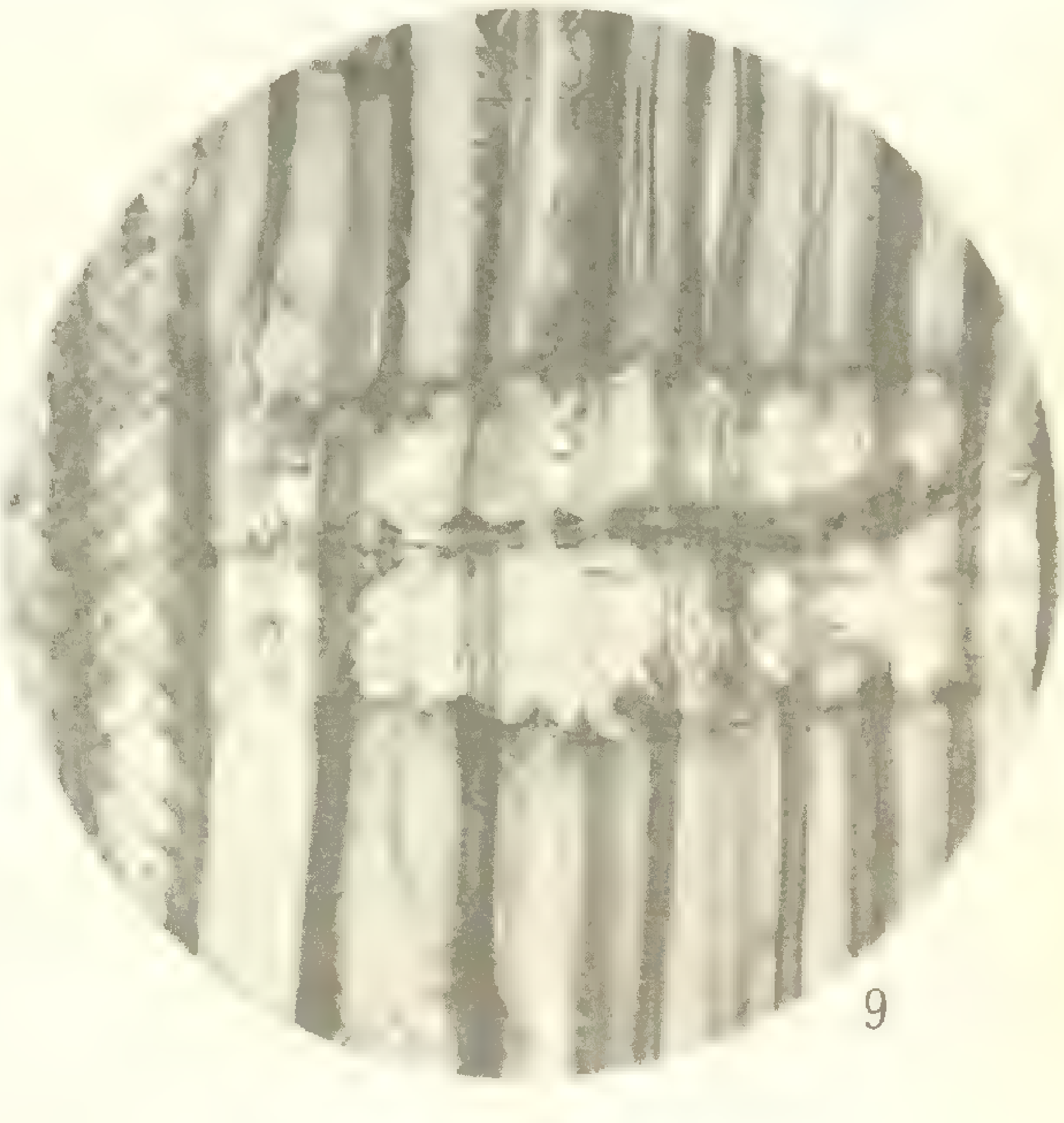
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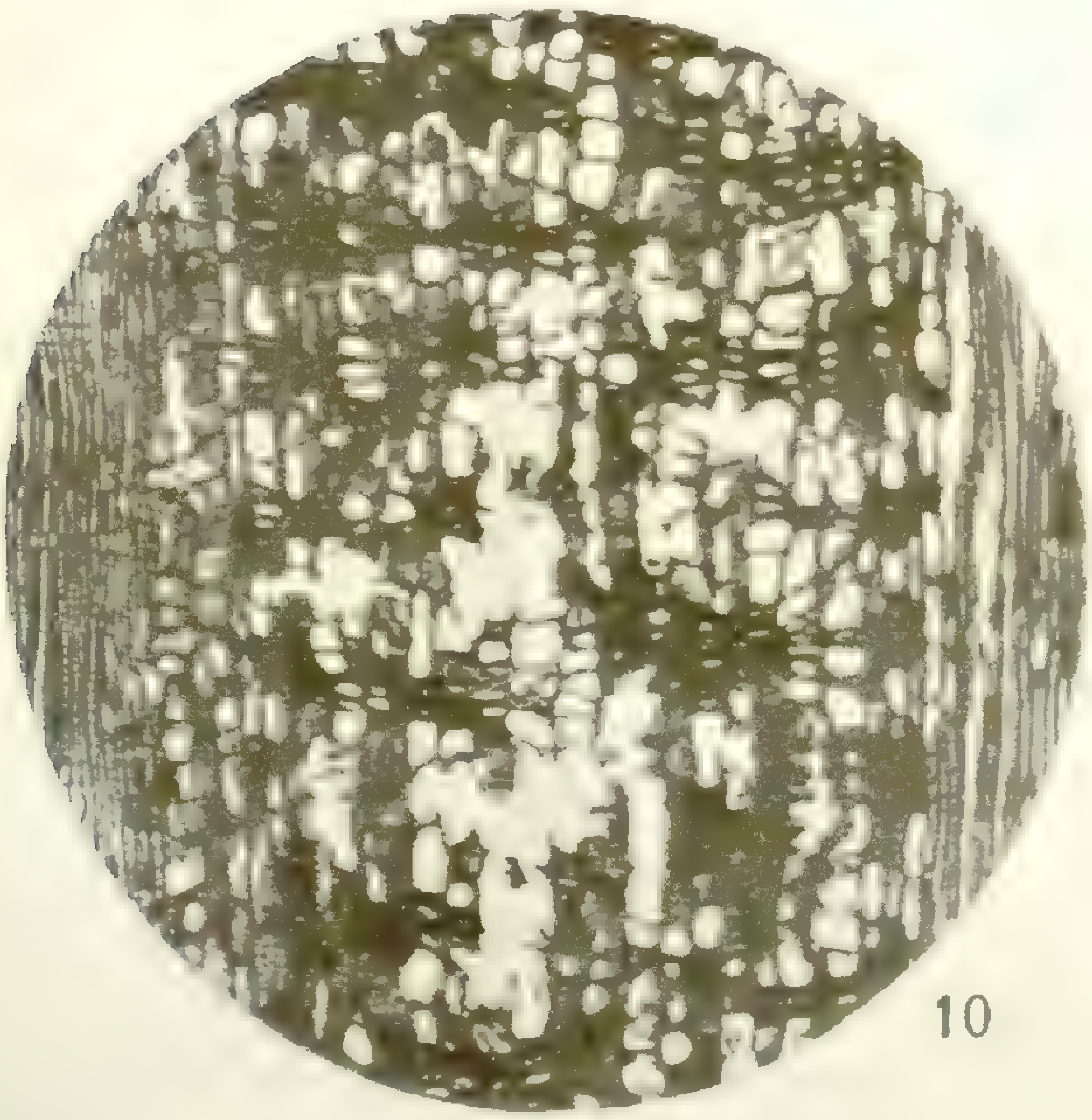
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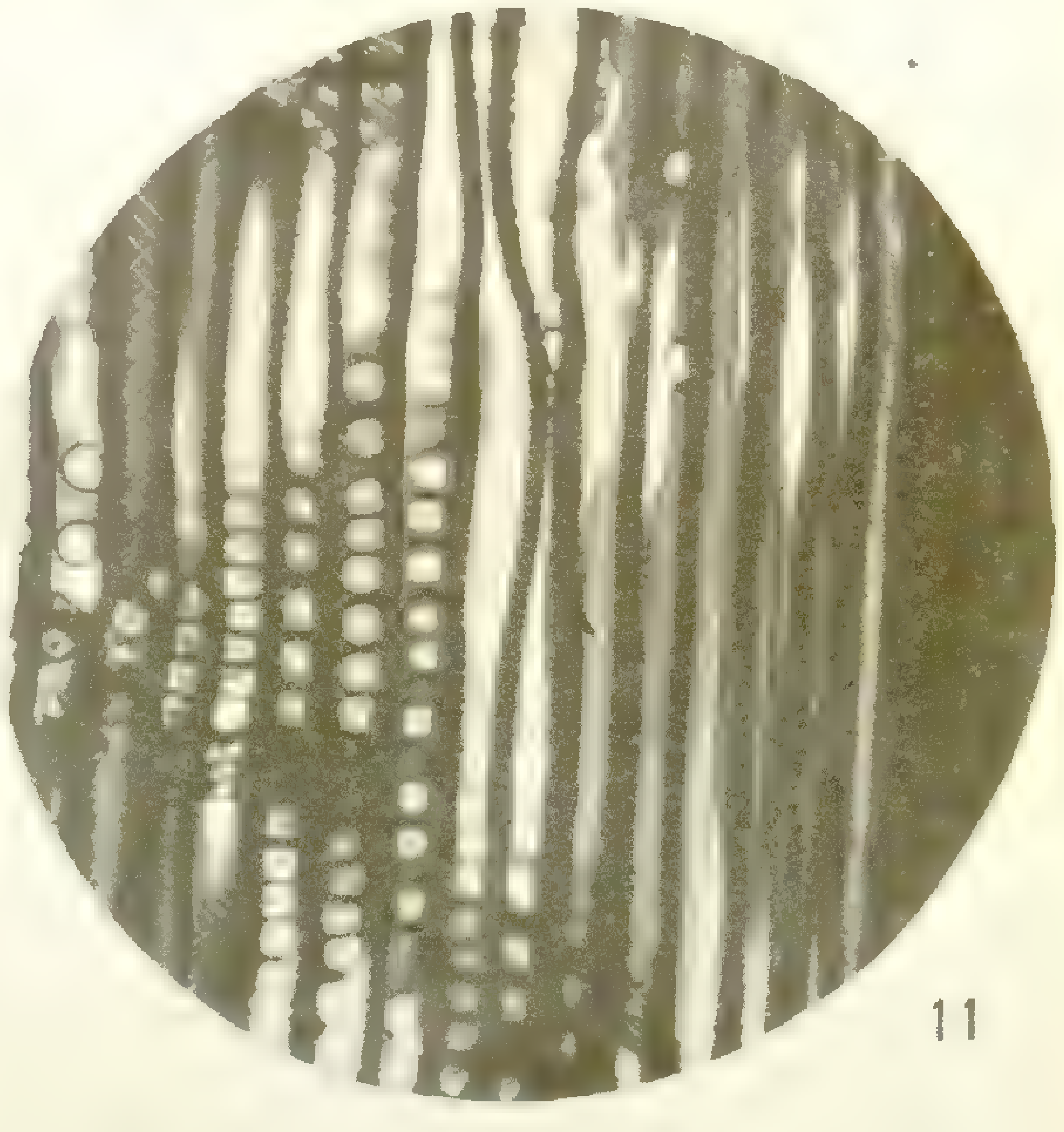
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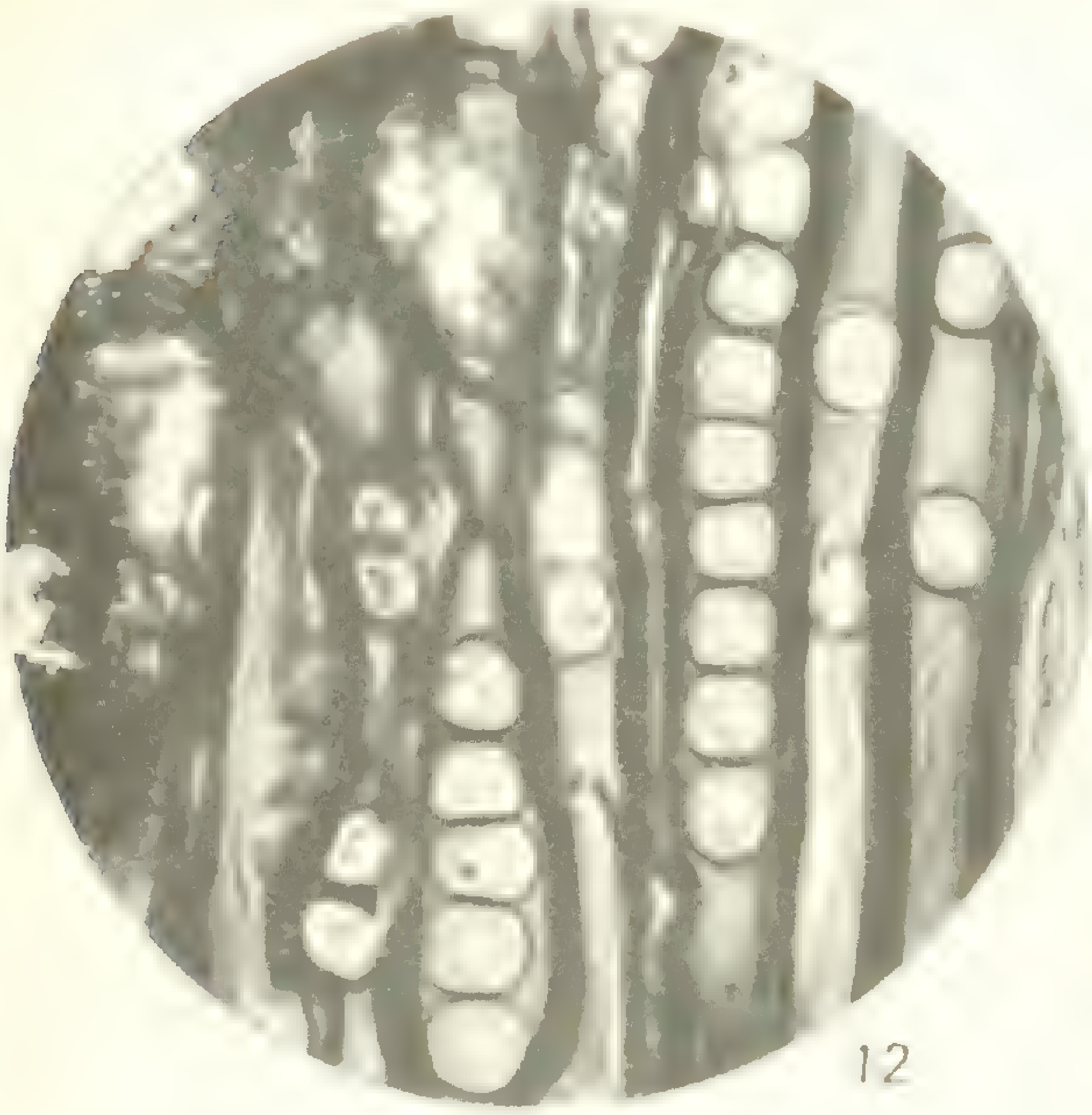
JEFFREY on ARAUCARIOPITYS



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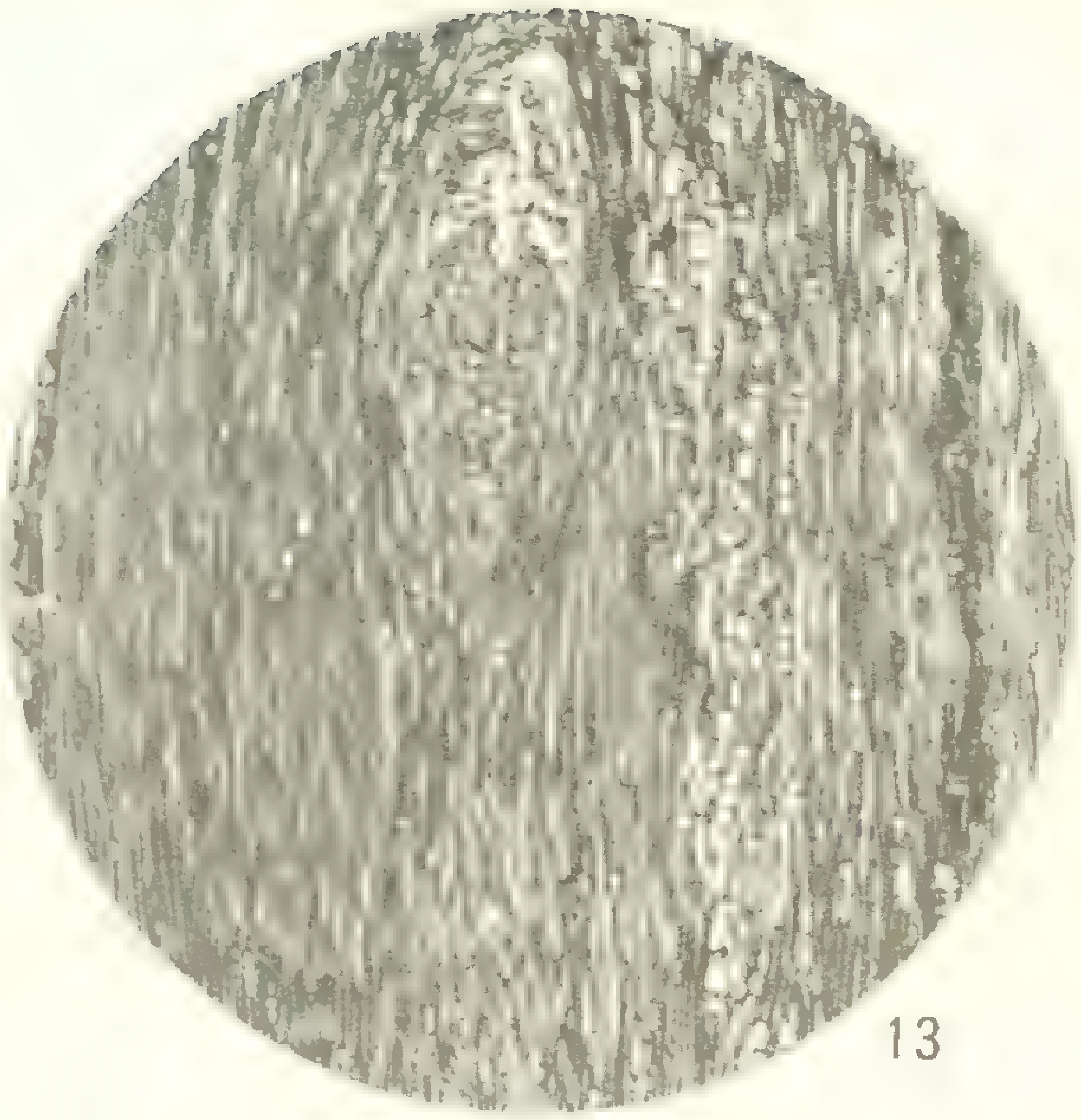

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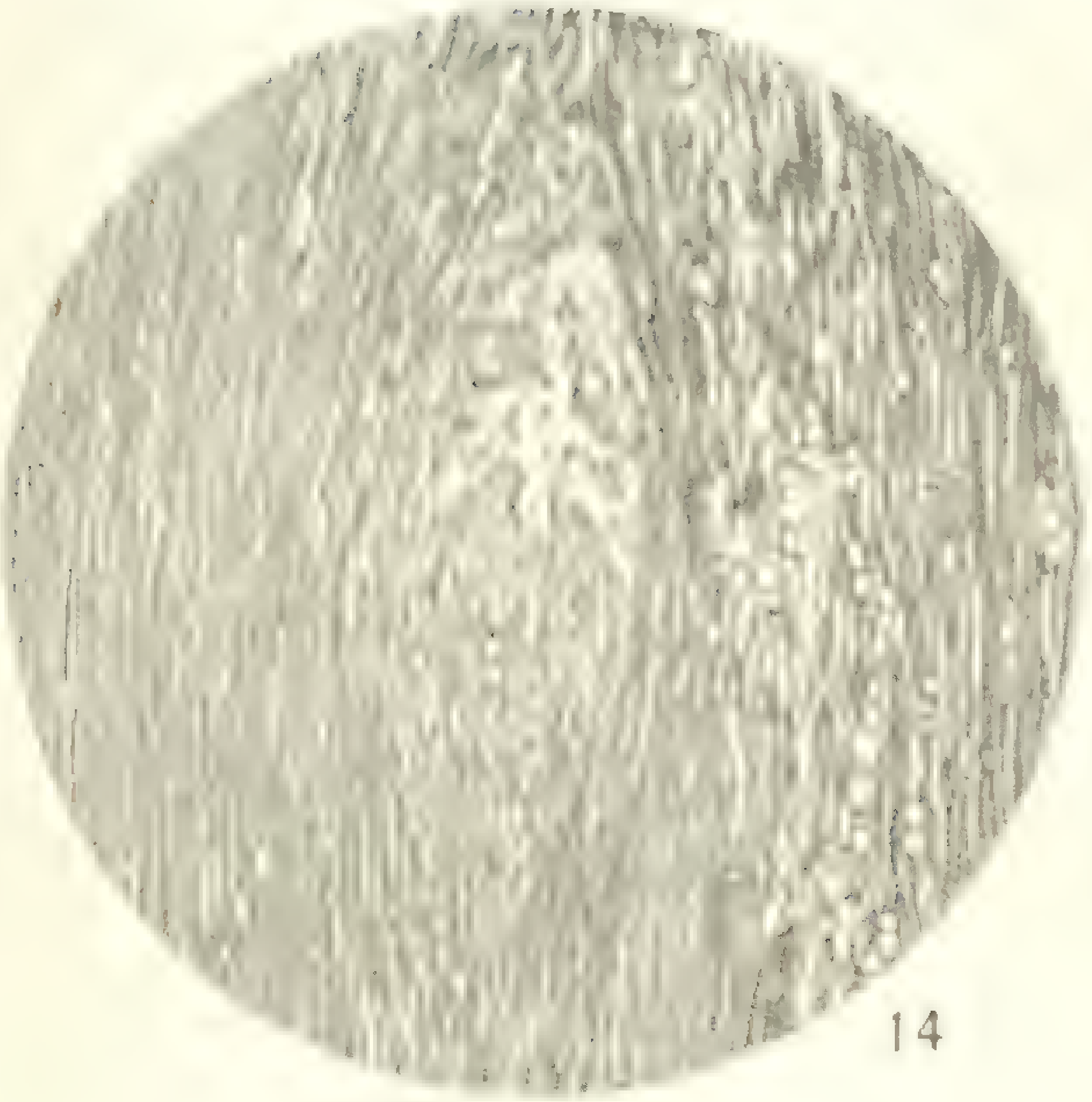

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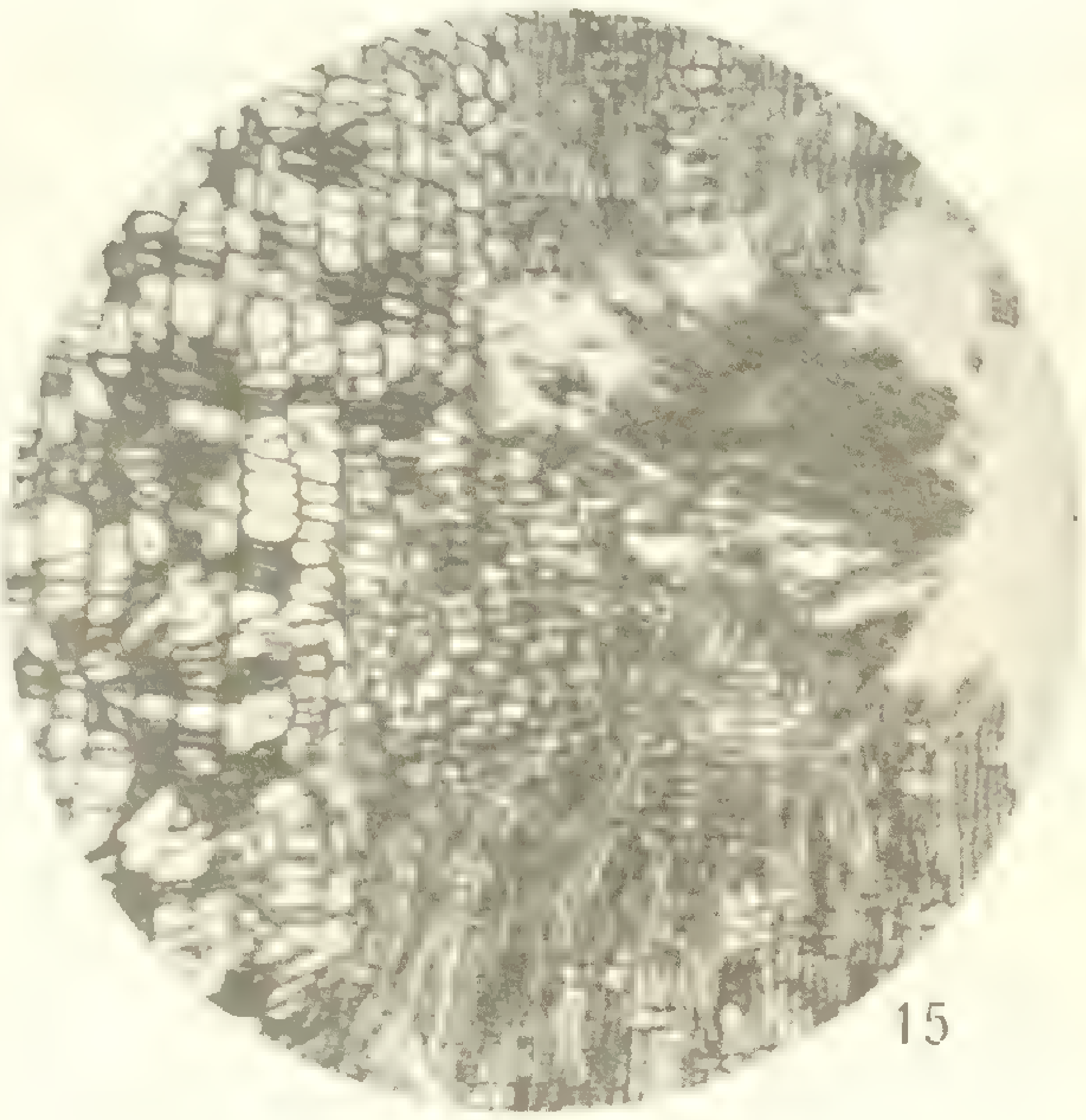

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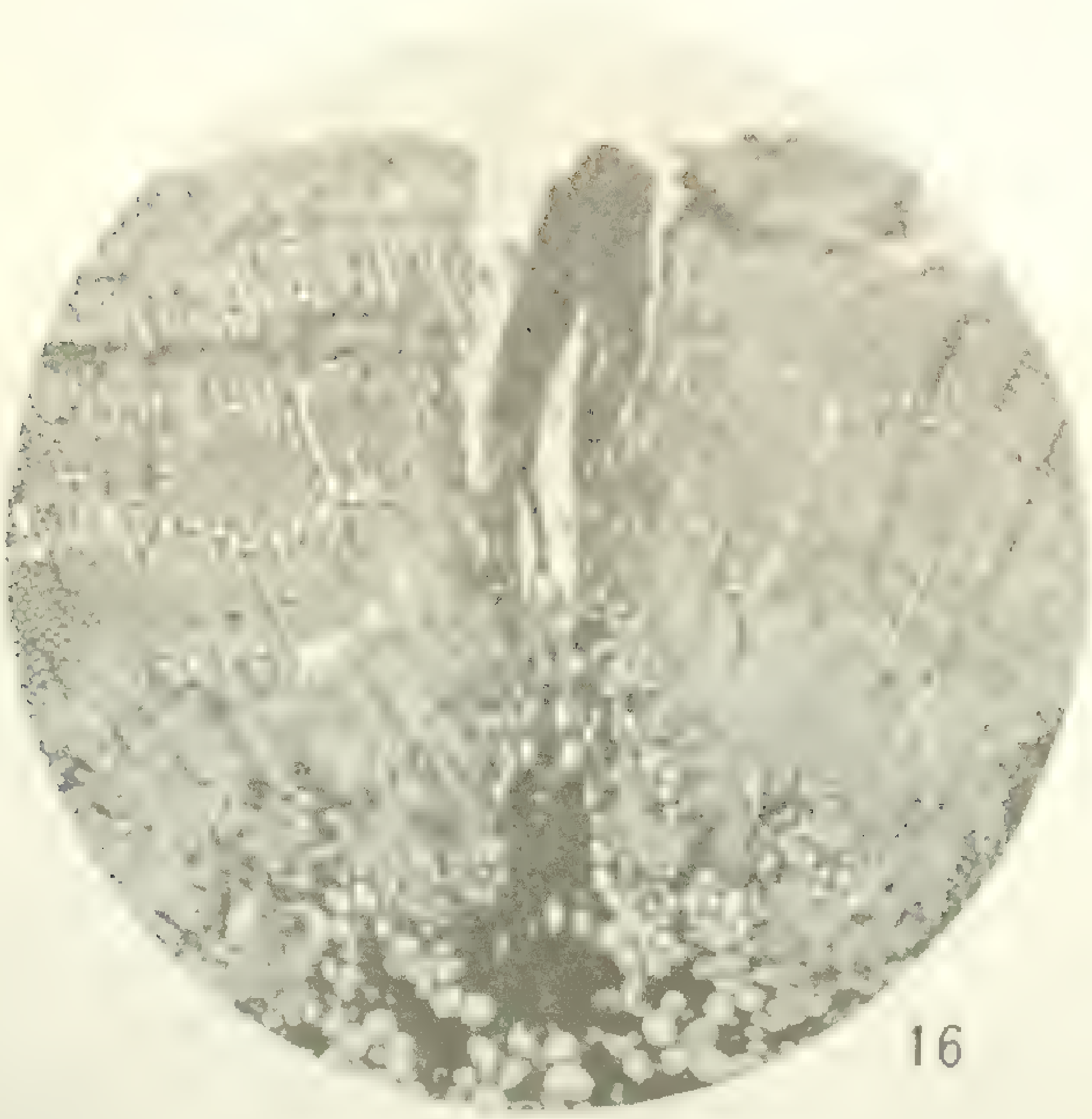

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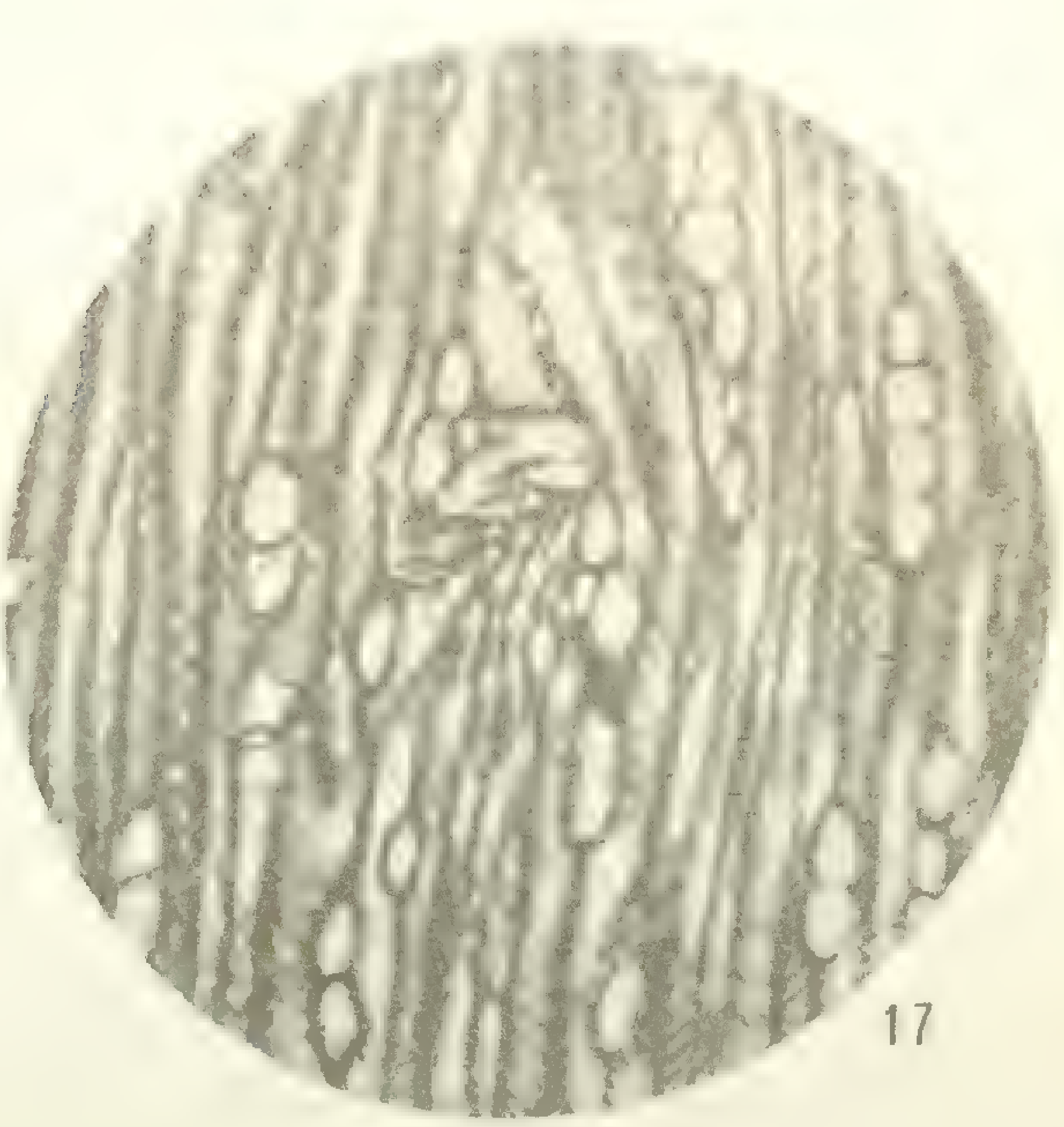

17

JEFFREY on ARAUCARIOPITYS

DIFFERENTIATION OF SPOROCARPS IN AZOLLA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 105

WANDA M. PFEIFFER

(WITH PLATES XXXI AND XXXII)

A summary of the work on Azolla up to 1844 may be found in GRIFFITH'S (1) account of Azolla and Salvinia. Working on *Azolla pinnata*, GRIFFITH began his account with the development of the sporocarps. The earliest stage described showed two sporocarps within a hoodlike involucre. Each sporocarp consisted of a cup-shaped integument and a cellular body, the "nucleus,"[1] which was surrounded by the "integument"[2] and projected from it. Later the "nucleus" elongated and the "integument" grew out so rapidly as finally to inclose it. At a still later stage, simple capitate "filaments"[3] of cells developed about the base of the "nucleus." Up to this point, the development in the two organs had been similar. After this, there might be a development of either the "nucleus" or the cellular projections about its base, but in no case did both continue growth. In cases where the further growth was in the "nucleus," GRIFFITH describes it as developing into the "so-called male organ" of former writers. This organ consisted of an egg-shaped body, bearing a calyptra and containing a large yellow sac capped by a peculiarly stratified body. The first change in the development here was a granular condensation of the materials of the "nucleus." When, on the other hand, only the "so-called female organs" developed, the first step was the appearance of a granular mass in the swollen tip of each of the "filaments," which had appeared in centrifugal order about the base of the "nucleus."

Nearly thirty years later (1873), STRASBURGER (2) wrote *Ueber Azolla*, in which he gave a full account of the mature sporocarps, but said little about their development. He found in the early stages of the megasporocarp a single sporangium developing, and when later he found only one megaspore in the mature sporocarp he naturally inferred that only one sporangium had appeared. Referring to GRIFFITH'S work, STRASBURGER suggested that in case more than one sporangium did appear in a sporocarp, it is more likely that all sporangia should have appeared simultaneously, and that later those about the base of the large central sporangium should have aborted. In the microsporocarp he found microsporangia, in numbers as high as forty, arising from a short "columella." He further said that he found no sign of the club-shaped ending of the columella which MEYEN had described earlier.

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[1] From GRIFFITH'S figures it is evident that this "nucleus" is the megasporangium.

[2] The "integument" is the sporocarp wall.

[3] These "filaments" are evidently the young microsporangia, which arise from the massive stalk of the megasporangium.

In 1889 STRASBURGER (**3**) reinvestigated the subject. According to that account, the primordia of both male and female sori are alike, since in each case there arose at first a short-stalked "macrosporangium" at the apex of the columella. In the "macrosporocarp" this went on developing, but in the microsporocarp its growth was soon inhibited, while from the columella beneath it microsporangial primordia were constantly arising. He suggested that the development of one or the other might depend upon the method of nutrition.

In 1893 CAMPBELL (**4**), referring to *Azolla filiculoides*, wrote:

> For some time each sporocarp rudiment grows by a three-sided apical cell. Next a slight outgrowth is observed near the base of the young sorus, which forms a ring-shaped projection; this is the beginning of the indusium or sporocarp wall. . . . . From this point, the two sorts of sori differ. In the macrosporic one, the apical cell forms at once the body of a single sporangium; in the microsporic it forms a columella, from which latter the microsporangia appear as lateral outgrowths.

In speaking of the megasporocarp he said:

> When the sporangium is about half grown, the outer cells of the very short stalk grow out into short papillae, which apparently are abortive sporangia, as they show divisions which recall the earlier ones in the macrosporangium. Their position corresponds to that of the microsporangia, so that although formed much later than the macrosporangium, it is pretty safe to assume that Azolla is derived from some form in which, as in Salvinia, there are several macrosporangia in the sporocarp. . . . . In the male sorus, as we have already seen, the apical cell of the young rudiment does not form a sporangium, but gives rise to a central columella or placenta from which microsporangia arise laterally, while the end projects as a cylindrical body. This latter was observed by MEYEN, but STRASBURGER seems for some reason to have overlooked it. I found it in all of my sections of the male sorus.

In 1898 GOEBEL (**5**) again investigated the method of sporocarp development in *A. filiculoides*. He accepted STRASBURGER'S later account of the development of the microsporocarp, but in the megasporocarp he found in the later stages of development primordia of microsporangia which had aborted.

In CAMPBELL'S revised edition of *Mosses and ferns* (**6**, 1905), he refers to GOEBEL'S account and states that "in the microsporangial sorus the apex of the receptacle, which probably represents an abortive macrosporangium, forms a columella, from whose base the microsporangia develop." He uses the illustration of the microsporocarp which he had used in the original paper, and shows the columella as a club-shaped body which has little resemblance to a sporangium.

INVESTIGATION

Working on *Azolla caroliniana*, I have traced the development of the sporocarp, paying particular attention to the stage at which microsporocarp and megasporocarp are definitely differentiated.

The youngest stage in which the sporocarp can be readily recognized shows a young sporangium consisting merely of an apical cell and a short stalk, about whose base there is a ringlike projection (*fig. 1*). This sporangium, which holds the central position in the mature sporocarp, is the megasporangium, and is of the ordinary leptosporangiate type.

The projecting ring of cells about the base of the sporangium, by subsequent growth outward and upward, forms the wall of the sporocarp. Growth of the sporangium and growth of the sporocarp wall go on simultaneously, so that by the time the primary tapetal cells are cut off in the capsule of the sporangium, the two-layered sporocarp wall stands almost as high as the sporangium (*fig. 3*). While the development of the capsule of the sporangium has gone on in the regular leptosporangiate way, there has been no such elongation of the pedicel as might be expected. The divisions of the cells of the pedicel, for the most part, have been anticlinal rather than periclinal to the apical cell, so that the stalk is massive, almost as great in diameter as is the capsule (*fig. 3*). Growth in the capsule now continues in the usual way until there is finally a sporangium having one layer of wall cells and a single layer of tapetal cells surrounding a mass of eight megaspore mother cells in synapsis. There is no trace of an annulus of any sort to be found either at this or any later stage. By this time the sporocarp wall has usually grown up so as almost to inclose the sporangium, while the stalk of the sporangium is likely to be at least four or five cells in diameter (*fig. 4*). While the mother cells are in synapsis, still forming a compact tissue surrounded by a layer of tapetal cells, some of the outer cells of the sporangium stalk enlarge so as to form short papillae (*fig. 5*). These enlarged cells have nuclei larger than those of the other stalk cells, and very soon it becomes evident that each of them is the apical cell of a young sporangium (*fig. 6, mc*). This is the first appearance of microsporangia in the sporocarp. Shortly after the microsporangia appear, the walls of the tapetum in the megasporangium disappear, leaving tapetal nuclei free in a mass of cytoplasm. Surrounded by this tapetal cytoplasm and nuclei, the megaspore mother cells have now separated from each other and become rounded off (*fig. 6*).

In a few cases the growth of the megasporangium is inhibited at this point. When this occurs the megaspore mother cells become shrunken, the tapetal nuclei appear small and more densely granular than in the healthy sporangia, and the cytoplasm takes on a coarse, loosely granular appearance. As this breaking down goes on in the megasporangium, more and more microsporangial primordia appear at its base. This, however, is not the usual course of events. Ordinarily the growth of the megasporangium is not inhibited until after it has passed the spore mother-cell stage.

In almost every case, the megasporangium continues its growth in size while the young microsporangia are developing at its base. Finally the megaspore mother cells divide simultaneously (*fig. 7*) to produce the eight tetrads (*fig. 8*). Even while this division of the megaspore mother cells is taking place, growth in the microsporangia continues, as is readily seen by the fact that cell division sometimes takes place there (*fig. 7, mc*). It is therefore after the formation of the megaspore tetrads (*fig. 8*) that the critical stage in the development is reached.

At this stage the sporocarp wall, which consists of only two layers of cells, has grown up beyond the apex of the megasporangium and has become almost if not completely closed by the greater elongation of the cells of the outer layer. The general shape of the sporocarp is oval, flattened on one side, and with a beak of enlarged cells at the top. Just inside this wall one often finds unattached filaments of Anabaena lying in the space above the megasporangium. At the base of the sporocarp there arises a massive stalk bearing sporangia. Of these sporangia, the oldest, which holds the central position, is the megasporangium, while the very young microsporangia form one or more whorls about its base. Within the megasporangium wall, of a single layer of cells, is found a mass of cytoplasm in which a large number of small nuclei, of tapetal origin, are lying free, and in the center, surrounded by the most densely granular of this cytoplasm, eight tetrads of spores are lying free from each other.

The question now is whether the megasporangium or the group of microsporangia, all of which are apparently vigorous, shall go on developing. If the megasporangium develops, there will be a megasporocarp; while if the microsporangia develop, there will be a microsporocarp.

In the megasporocarp, thirty-one of the megaspores abort, while one, which usually holds the central position in the sporangium, continues growth (*fig. 9*). The megasporangium increases in size, but there is no further elongation of the stalk, and the young microsporangia at its base cease their growth. As the megasporangium increases in size, it finally completely fills the sporocarp, and the young microsporangia are squeezed down against the stalk until they are hardly recognizable. An abnormal condition, which I found in two megasporocarps, shows two of the megaspores developing, while only thirty abort.

In the microsporocarp, the abortion of the spores in the megasporangium goes a step farther than in the megasporocarp, and we find all thirty-two megaspores aborting. Within the megasporangium the cytoplasm takes on a coarsely granular appearance, the tapetal nuclei are dense shrunken masses, and the megaspores, which may hang together in tetrads or may fall apart as separate spores, are shrunken and shapeless (*fig. 10*). As this abortion goes on, the stalk of the megasporangium elongates somewhat and new microsporangial primordia continue to appear below the older ones, which are increasing rapidly in size. The microsporangia arise in basipetal succession, have long slender stalks, and each sporangium develops sixteen spore mother cells. As the growth of the stalks in length and of the capsules in size continues, there is a consequent broadening of the sporocarp, which makes of the mature microsporocarp a round body, quite different from the more elongated megasporocarp. By the time the oldest of the microsporangia have reached the mother-cell stage, the megasporangium has usually collapsed, so that unless one happens to get a median section of the sporocarp (*figs. 11, 11a*) it is likely to escape notice. However, I found several microsporocarps in which this collapse of the megasporangium did not occur. In these cases the cytoplasmic contents of the megasporangium had broken down and had to a large extent been resorbed, but the sporangium wall remained turgid, while the cells of the stalk at the base of the sporangium had grown up into the cavity left by the breaking-down of the cytoplasm (*figs. 12, 13*). In one case (*fig. 13*) this growth had continued until the sporangium was nearly filled with vegetative tissue.

DISCUSSION

While GRIFFITH, in 1844, interpreted the megasporangium as a male organ and the microsporangia as female organs, as R. BROWN and MEYEN had before him, he gave an accurate account of the order in which the various structures of the sporocarp appear. Since the appearance of STRASBURGER'S *Ueber Azolla*, writers seem largely to have overlooked GRIFFITH'S work. Doubtless this is due to the fact that STRASBURGER, who worked largely on the very early and the mature stages of the development, without catching the intermediate stages, suggested that probably GRIFFITH'S account would not hold true, since it seemed more probable that the sporangia would appear simultaneously in the megasporocarp as they did in the microsporocarp. It is interesting to note that sixteen years after *Ueber Azolla* appeared, STRASBURGER again gave an account of Azolla, in which he affirms that the primordia of the two sporocarps are alike, since each begins with the development of a megasporangium, which in the microsporocarp soon aborts. It is evident that he no longer thought that the development of sporangia in the microsporocarp is simultaneous, and so his former inference, that probably the megasporocarp is like the microsporocarp in this particular, no longer has any weight.

CAMPBELL, writing four years after the appearance of STRASBURGER'S second paper, has evidently not given close attention to this later account of the development, or he might have been led to make a more careful study of the columella, which he found in all his preparations of the microsporocarp. That this columella actually represents an abortive megasporangium seems not to have occurred to him, although STRASBURGER'S paper would have suggested it. The nearest approach that I found to such a columella as CAMPBELL figures was in the few cases where the vegetative cells of the stalk had grown up into the cavity left by the collapse of the cytoplasmic contents of the megasporangium (*figs. 12, 13*). Any section, except the median, of such a sporangium as that shown in *fig. 13*, would show merely a club-shaped mass of cells; but the median section shows very clearly the remains of the broken-down cytoplasm and nuclei.

To one who has noted the megasporangium beginning to develop in the microsporocarp and then aborting, the interpretation of the sporangial primordia about the base of the megasporangium in the megasporocarp as microsporangia is natural. CAMPBELL, having missed this first point, seems to have missed the second one also, since he infers that the sporangial primordia in the megasporocarp are megasporangial, and so to be compared with Salvinia. He overlooks the fact that in Salvinia the appearance of sporangia is much more nearly simultaneous than in Azolla.

Of all the accounts of Azolla, GOEBEL'S most nearly portrays the course of events as I saw it. Yet even he accepts STRASBURGER'S statement that the abortion of the megasporangium in the microsporocarp occurs early. While at first sight this would seem to be the natural course of events, abortion after the formation of the megaspores really carries the reduction in the megasporangium only one step farther than in the megasporocarp. Long ago STRASBURGER saw cases in the megasporocarp where two spores developed while thirty aborted. This condition, which I have seen a few times, was readily looked upon as a reversion to the condition in which more than one spore developed in the megasporangium. The abortion of all thirty-two spores in the megasporangium, which holds the central position in the microsporocarp, could be considered a further step in this reduction.

What causes the abortion in one case of thirty, in another of thirty-one, and in a third of thirty-two megaspores, is a question not easily determined. It would seem largely a matter of chance, since there is no external factor or group of factors responsible. Very often megasporocarp and microsporocarp lie side by side, having begun their development from two apical cells which were formed by the division of a single cell, and having continued growth with their surroundings as nearly alike as it is possible to make them. On the other hand, there is no internal condition that we can say, definitely, must be responsible for this. There is of course the possibility that the whole thing is a question of food supply, as STRASBURGER suggested. If there should be some change in the cells of the stalk below the megasporangium making them impermeable to any of the materials which are necessary for growth in the sporangium, the inhibition of growth there would be a natural result. That the food supply thus kept from the megasporangium should then be used for the further development of the microsporangium at the base, seems a plausible supposition. In cases where the cells of the stalk later grow up into the megasporangial cavity, one would have to suppose a regaining of permeability of the cells to food materials. Such changes in the cells from permeability to a given substance to impermeability and back to permeability are quite possible physiologically.

SUMMARY

1. The early development of megasporocarp and microsporocarp are exactly similar. Each begins development with a single megasporangium and a sporocarp wall. When the megasporangium has reached the stage in which eight spore mother cells are in synapsis, some of the outer cells of the stalk enlarge and become the apical cells of young microsporangia. Growth in the microsporangia and megasporangium now goes on simultaneously for some time. The tapetal walls of the megasporangium disappear and the mother cells separate from each other and round off, while the microsporangia at the base continue development, differing in appearance from the

megasporangium only in having long slender stalks and later forming sixteen rather than eight spore mother cells. Before the primary wall cell is cut off in the oldest of the microsporangia, the megaspore mother cells have divided simultaneously to form eight tetrads. Up to this point the development is the same, whether the structure is to be a megasporocarp or a microsporocarp.

2. Further development of the megasporocarp shows one of the thirty-two megaspores continuing growth, while the other thirty-one abort, and the microsporangia at the base of the megasporangium cease growth.

3. Further development of the microsporocarp shows all thirty-two megaspores aborting, while the young microsporangia increase rapidly in size and number. The megasporangium usually collapses so that it is not readily seen in the mature microsporocarp.

This investigation was carried on under the direction of Professors John M. Coulter and Charles J. Chamberlain, The University of Chicago.

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5. Goebel, K., Organographie der Pflanzen 2:488. 1898.
6. Campbell. D. H., Mosses and Ferns, Ed. 2, 412. 1905.

EXPLANATION OF PLATES XXXI AND XXXII

The figures were all made with a Zeiss camera lucida and in all cases, except *fig. 11a*, a Zeiss ocular 4 and Zeiss 2^{mm} objective were used, giving a magnification of 430 diameters after a ½ reduction is made in the reproduction.

Abbreviations: *a*, Anabaena; *am*, abortive megaspore; *as*, abortive megasporangium; *at*, abortive megaspore tetrad; *m*, functional megaspore; *mc*, microsporangia; *mcm*, microspore mother cells; *mm*, megaspore mother cell; *mt*, megaspore tetrads; *s*, sporocarp wall; *t*, tapetum.

PLATE XXXI

Figs. 1–8 give the stages in the development in which the megasporocarp and microsporocarp are similar.

FIG. 1. A very young sporocarp showing the beginning of the megasporangium and sporocarp wall.

FIG. 2. A stage later than *fig. 1*.

FIG. 3. A still later stage; the primary tapetal cells have been cut off in the megasporangium.

FIG. 4. A considerably later stage; the megasporangium is in the mother-cell stage, but no microsporangial primordia have yet appeared.

FIG. 5. A little later than *fig. 4;* the microsporangial primordia are appearing.

FIG. 6. The microsporangia have begun growth; in the megasporangium the tapetal walls have disappeared.

FIG. 7. The heterotypic division of the megaspore mother cells; growth in the microsporangium continuing.

PLATE XXXII

FIG. 8. A still later stage.

FIG. 9. A megasporocarp that can be readily recognized as such; microsporangia have ceased growth.

Figs. 10–13 show conditions found in the microsporocarp.

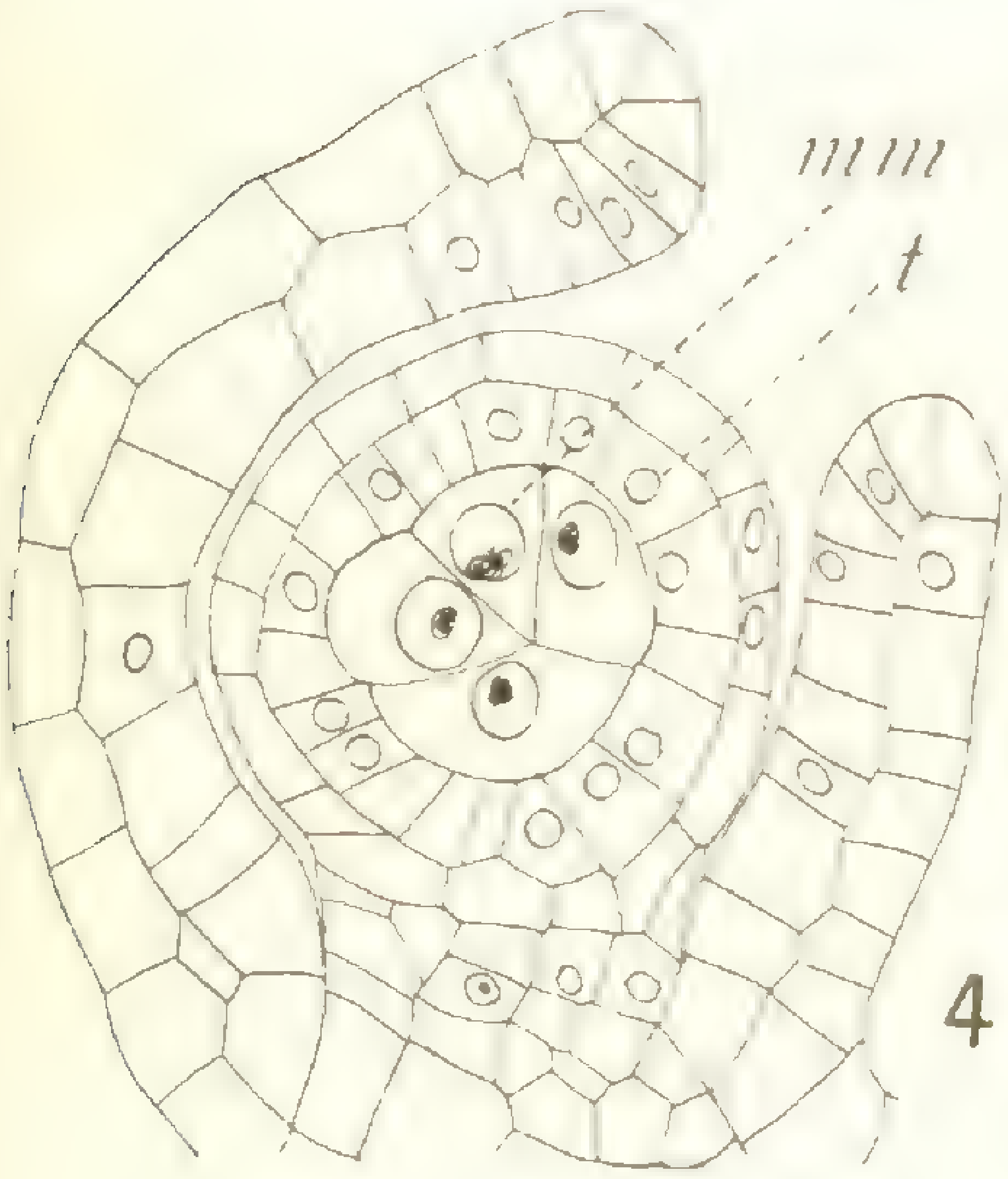
FIG. 10. A microsporocarp of about the same age as the sporocarp in *fig. 9;* the microsporangia are appearing in large numbers.

FIG. 11. The central portion of an older microsporocarp, showing the microsporangium with microspore mother cells, *mcm*.

FIG. 11*a*. An outline sketch of the whole sporocarp, a portion of which is enlarged in *fig. 11*.

FIG. 12. One of the abortive megasporangia, into which the cells of the stalk are beginning to grow.

FIG. 13. An abortive megasporangium which has been nearly filled by the upward growth of the cells of the stalk.



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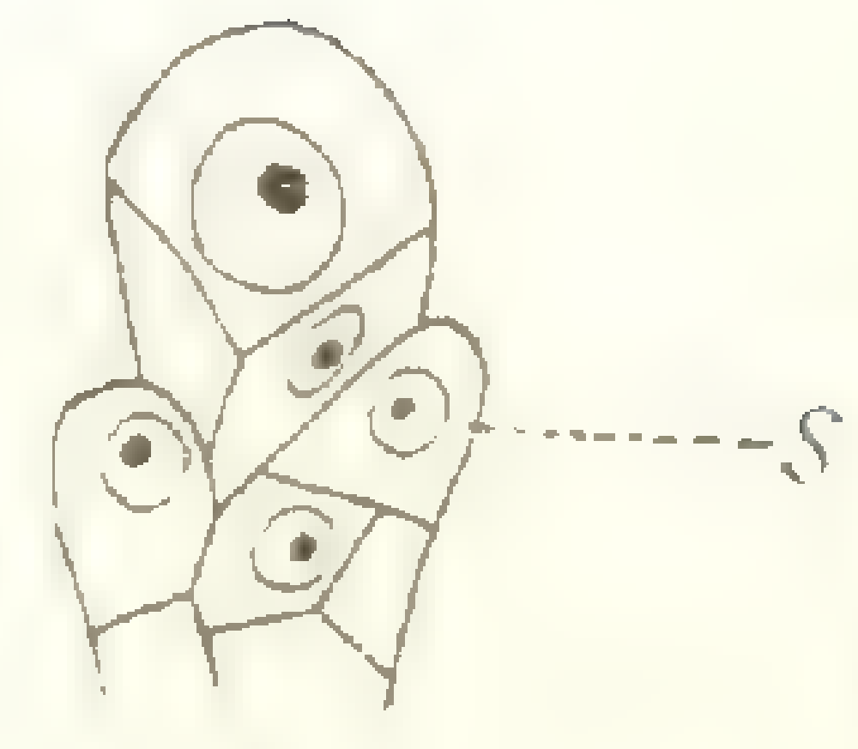

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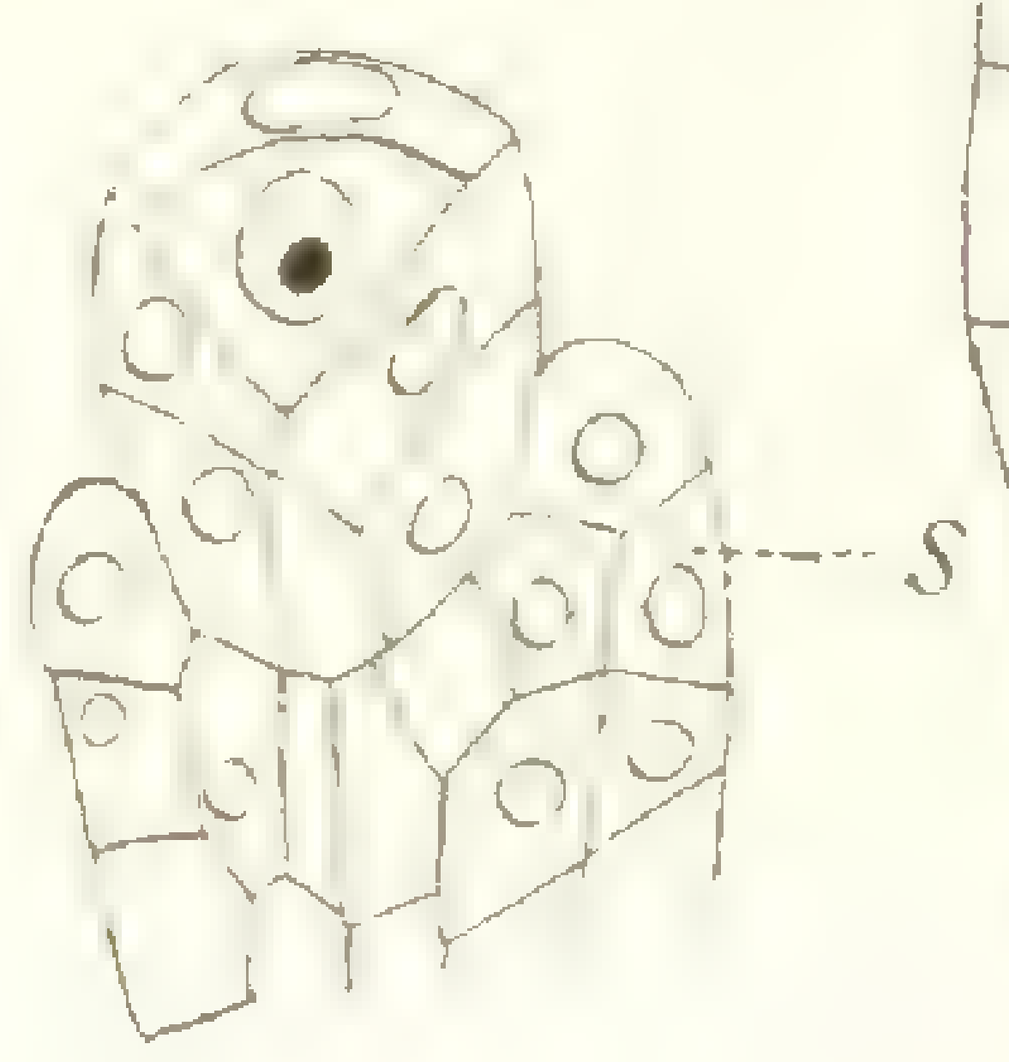

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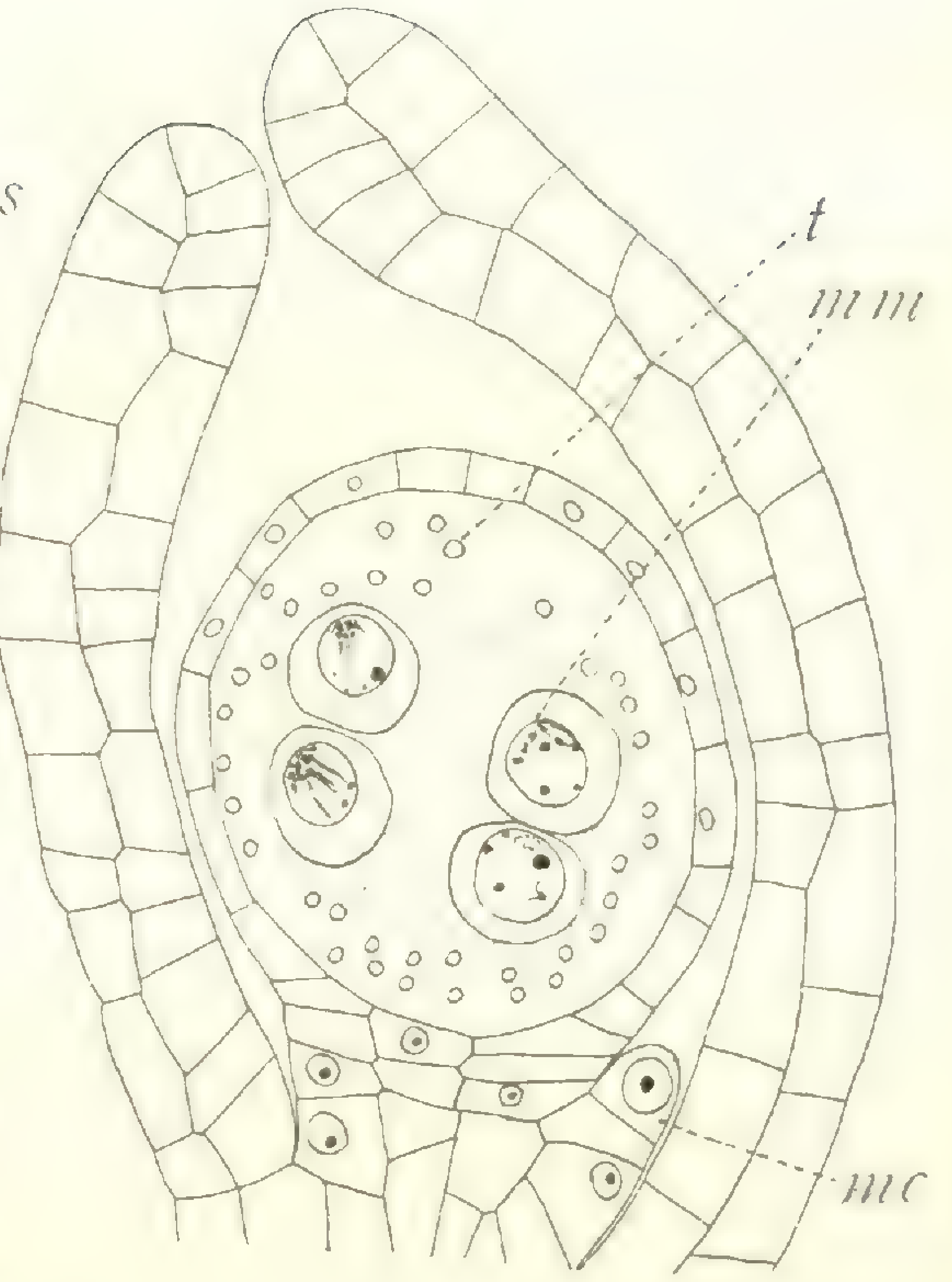

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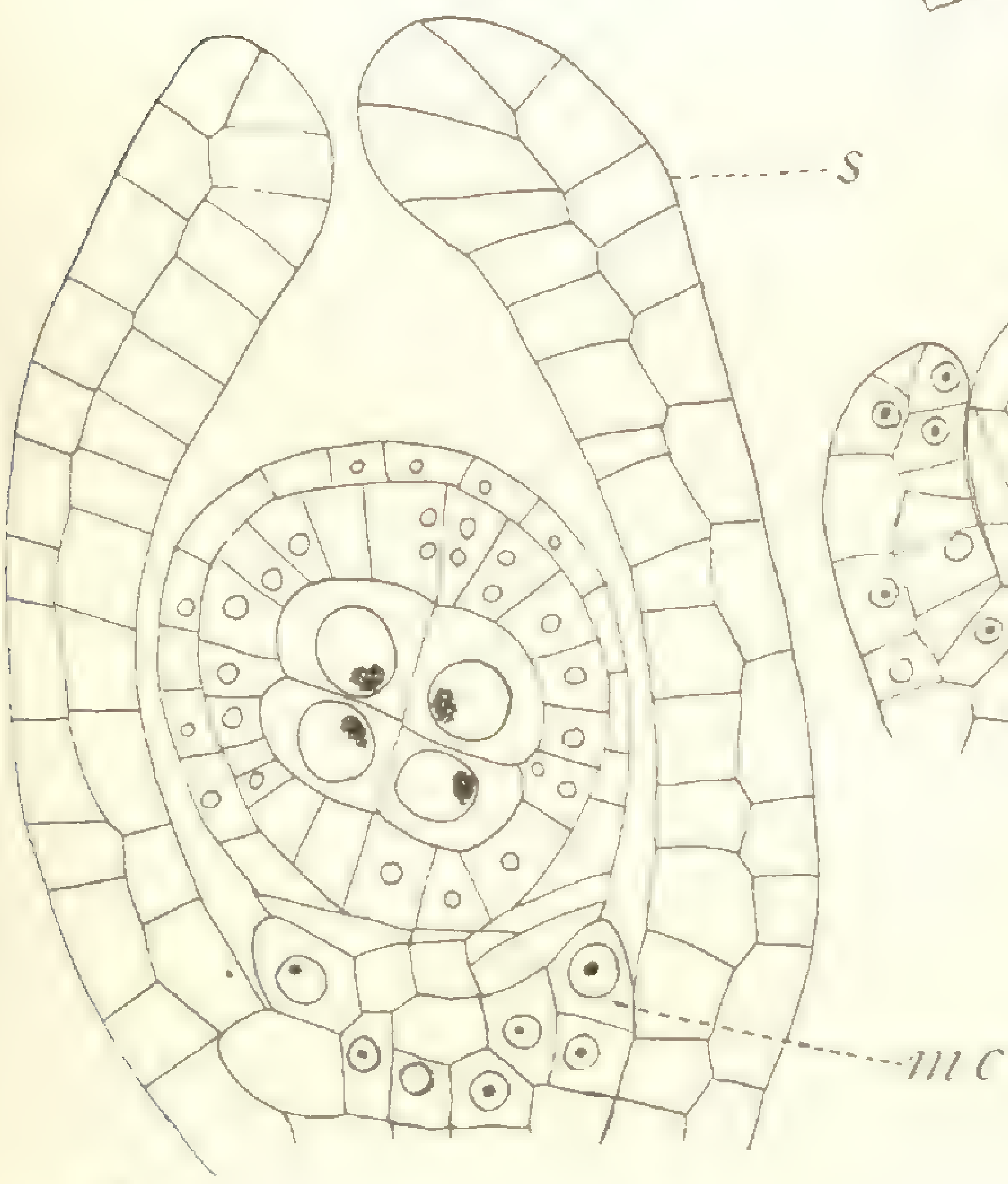

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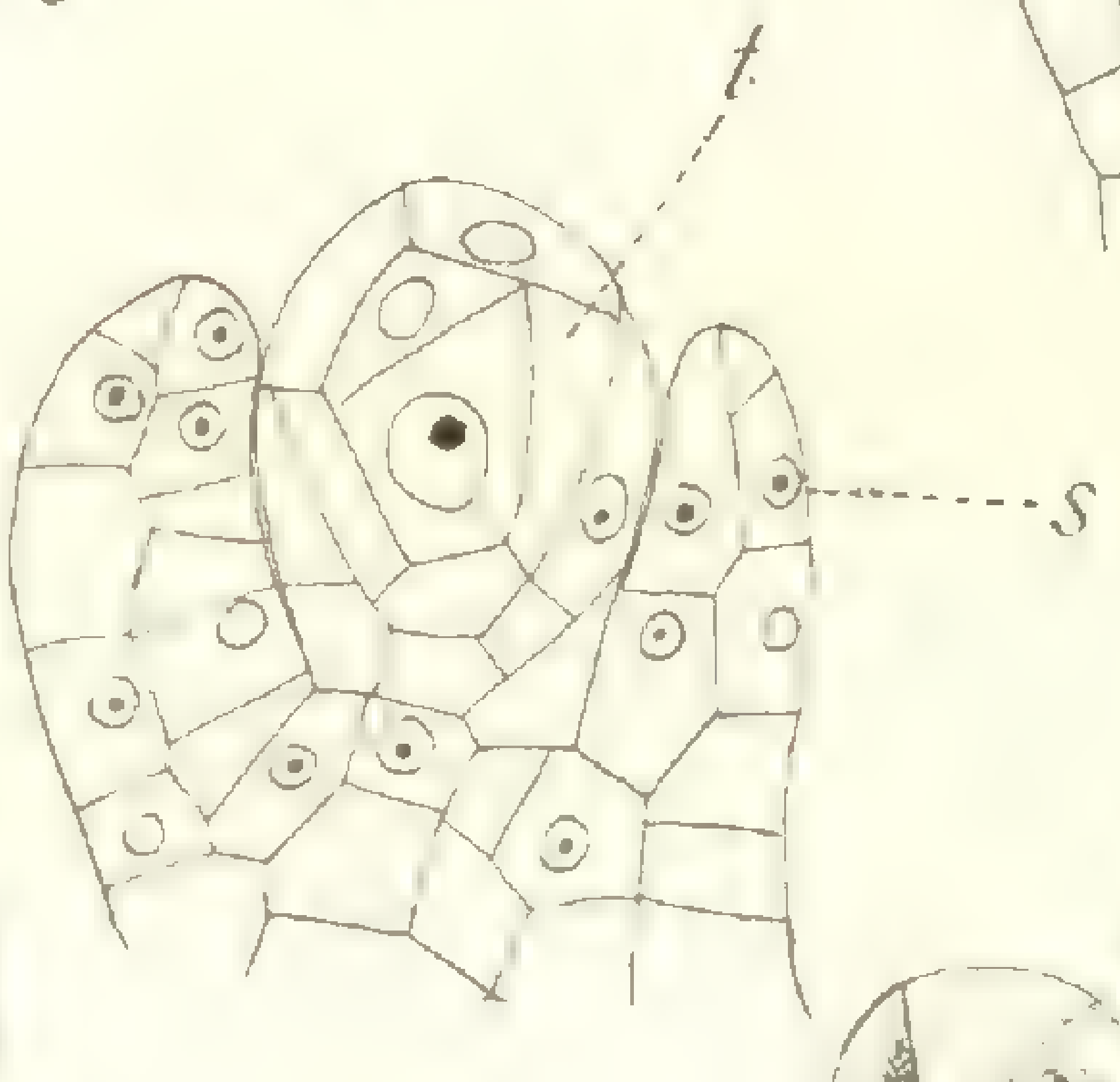

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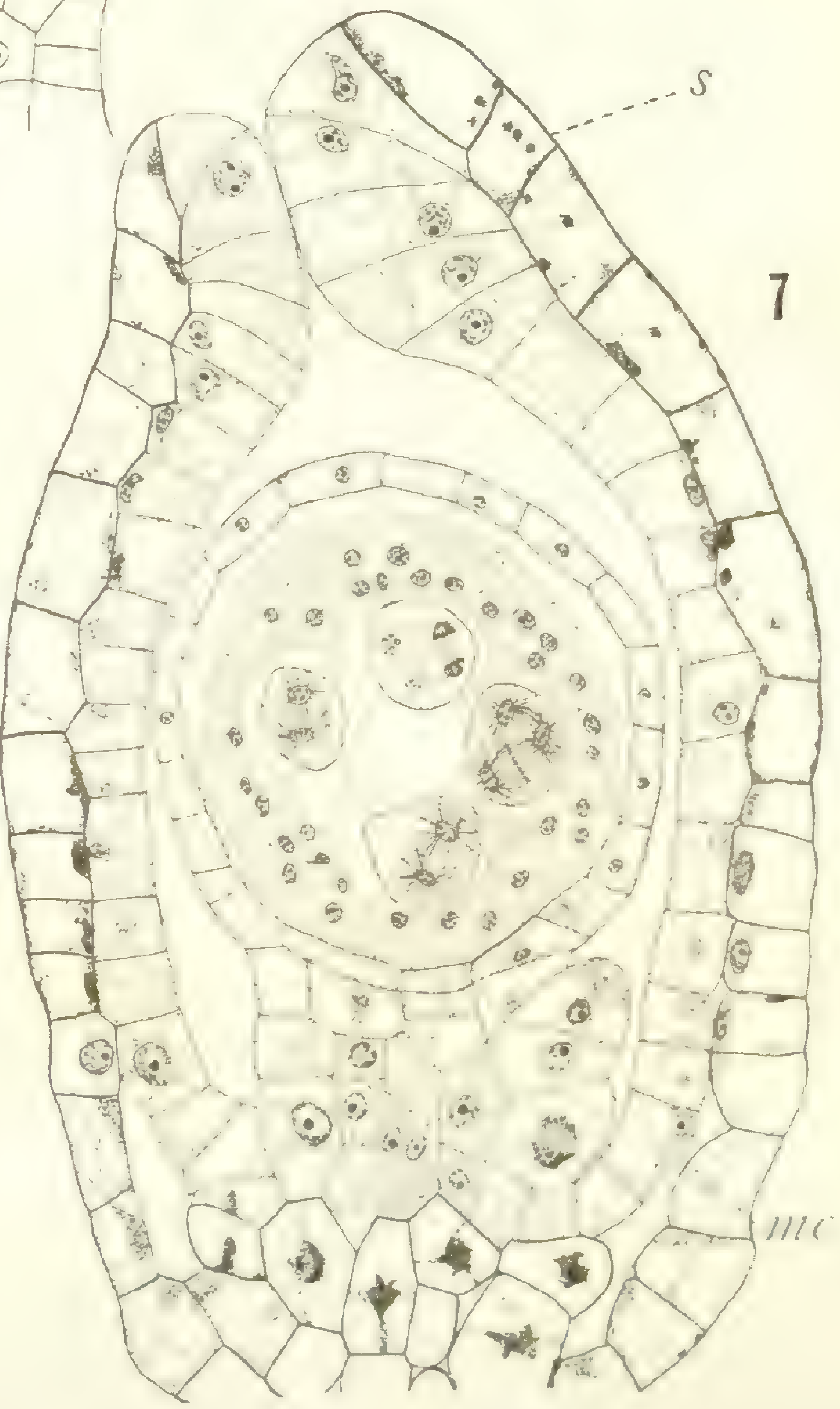

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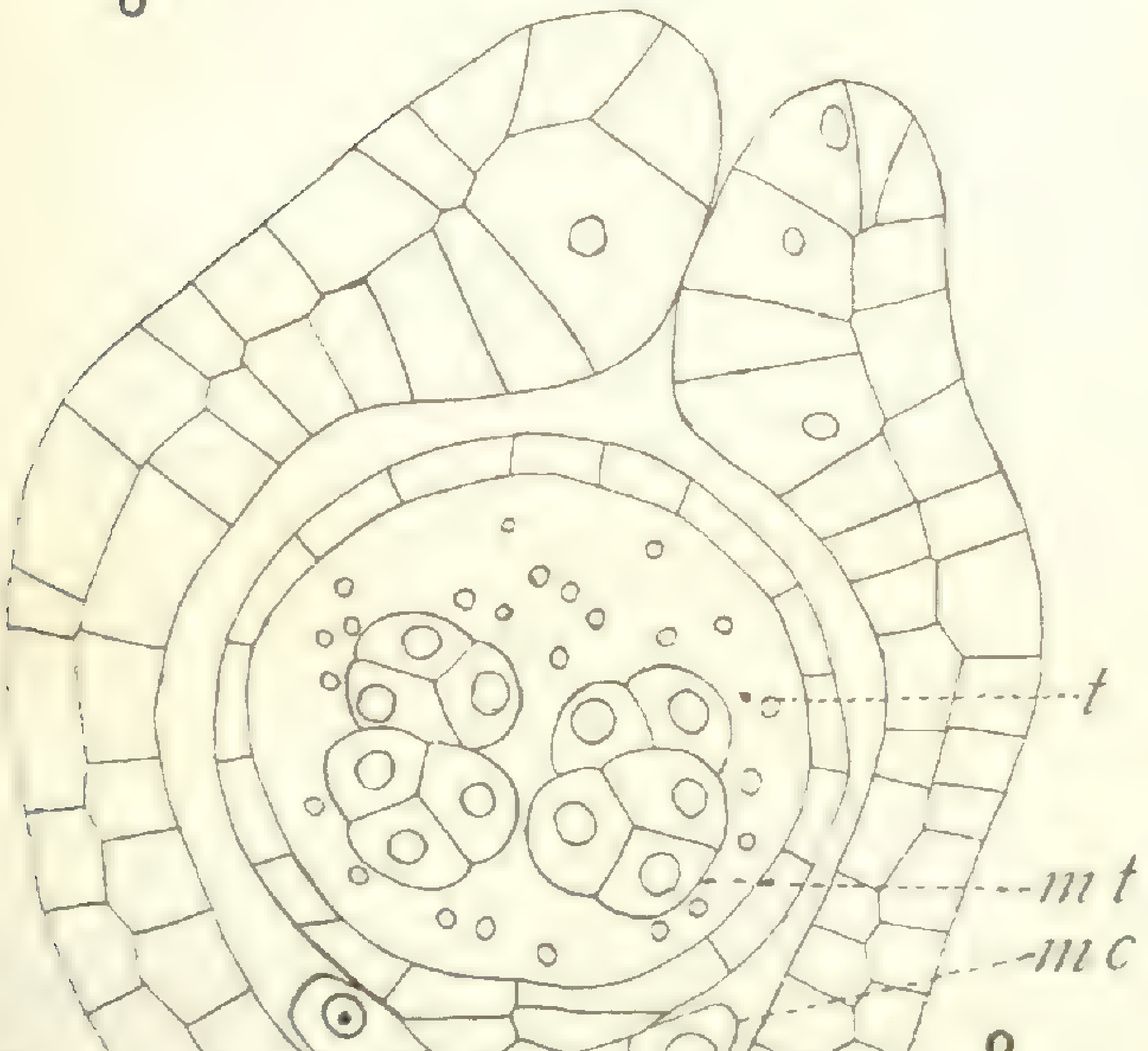

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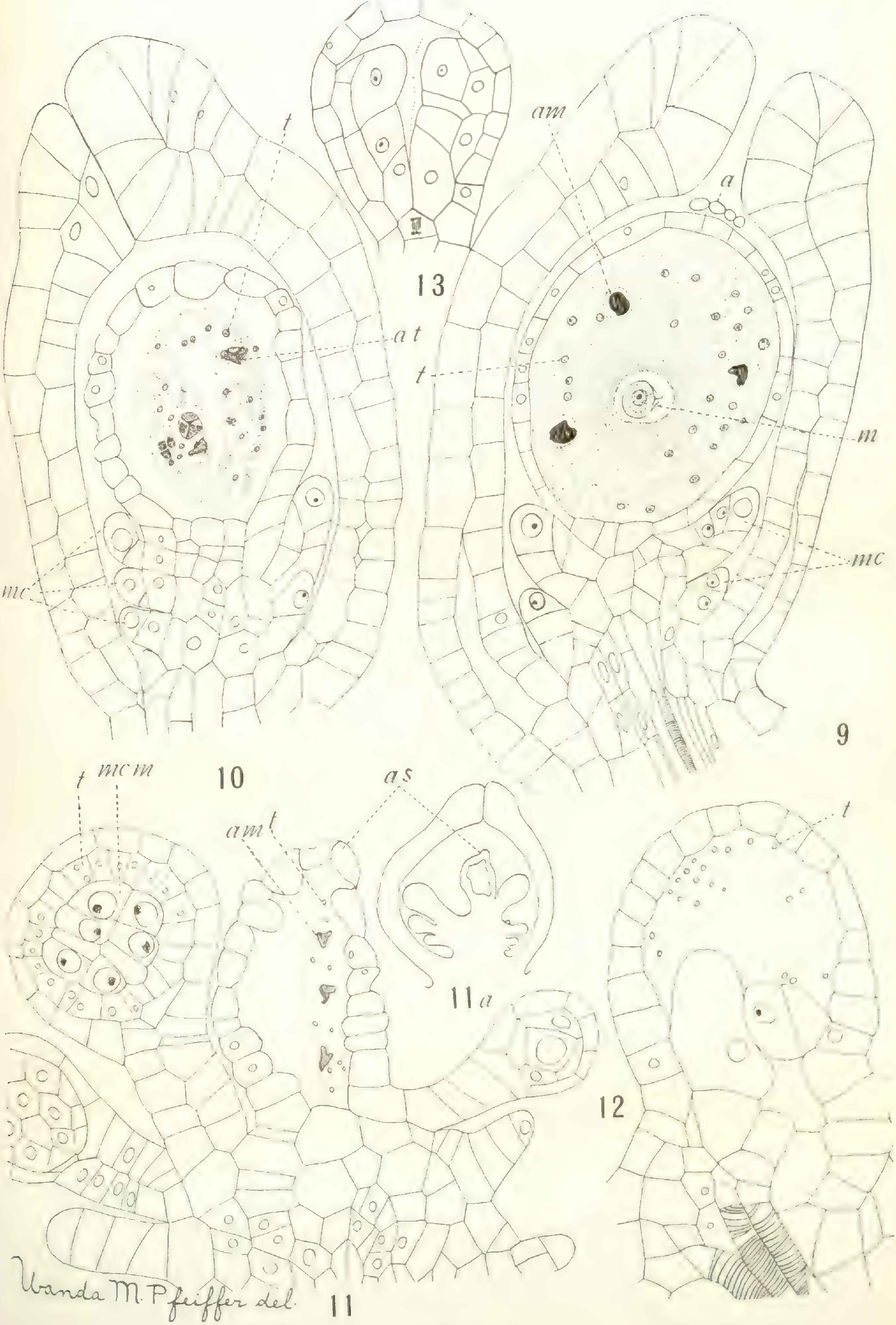
Wanda M. Pfeiffer del.

PFEIFFER on AZOLLA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PFEIFFER on AZOLLA

CURRENT LITERATURE

BOOK REVIEWS

The nature and development of plants

Dr. CURTIS[1] offers a new book with this title on a basis which must be regarded by anyone attempting to judge its merits. It is not intended as a textbook, says the author, but to give a point of view and to stimulate inquiry. A student who is thoroughly acquainted with *Principles of botany* by BERGEN and DAVIS would discover by examination of this text, as well as by reading the preface, that the book is intended for one of more limited secondary training. That the majority of college freshmen have in one way or another escaped or evaded adequate secondary training makes this effort by Dr. CURTIS very acceptable and practical. The author has used excellent judgment in the selection of material both for discussion and for illustration. So far as possible, plants which the student is likely to see or hear about are used. In order to awaken interest a narrative rather than an expositional style prevails, and the economic significance of several important features of plant life are emphasized in attractive connections. Associated with this style and plan there is apparent an effort to stimulate originality and independent reasoning.

The book is structurally simple, being without even a complete table of contents, but perfectly clear in plan and purpose. The introduction develops a conception of the cell as the unit of structure and of protoplasm as the physical basis of vital phenomena. Part I presents the outer and inner morphology of roots, stems, leaves, etc.; while Part II traces the phylogeny of the four great groups according to the older ENGLER and PRANTL classification. One is at once impressed with the unusual excellence of the illustrations of which there are over three hundred, in most cases original.

If one searches for defects, and this a critic is supposed to do, instances of faulty composition and inaccurate statement may be found. "The elements that compose any substances are held together with great energy owing to their mutual attraction for one another," is an unfortunate slip which disregards the numerous unstable compounds. "The transmission of hereditary characters may be stated as follows. Every feature of a plant or animal which we recognize in distinguishing them is due to hereditary substances derived from the parents." To what extent such a general statement is true cannot be said off-hand, though there is experimental evidence, not overlooked in the text, which renders such a generalization invalid. "The work of respiration is carried on more economically by green plants than by animals, since in the animal the CO_2 escapes in the breath as a waste product, while the plant uses the CO_2 during day time for the construction of foods." There is regrettable confusion here, involving comparison of incomparable processes. Carbon dioxide happens to be a waste product in animal metabolism, but in addition to this in the case of green plants it is also food material. The contrasting of the work of respiration in the two cases upon this basis is wrong, as the author well knows. As a matter of fact, we have no reason to believe that the work of respiration as done by plant protoplasm is more economical than that done by animal protoplasm.

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[1] CURTIS, CARLTON C., Nature and development of plants. 8vo. pp. 471. *figs. 342.* New York: Henry Holt & Co. 1907. $2.50.

That this book successfully meets the demand intended to be supplied by the author is certain, and this is abundant justification for anyone who has the courage to run the gauntlet with a new book.—RAYMOND H. POND.

Evolution in the potato beetles

Although the work of Professor TOWER[2] on Leptinotarsa deals with a group of animals, his book should not be overlooked by botanists on that account. Probably no work since the appearance of DEVRIES' *Mutationstheorie* is more worthy of careful study. The contribution is essentially along experimental lines, backed by years of observation in the field and laboratory. Many of the problems, if not solved, are seen in clearer light, and at least some of the mooted questions may now be dismissed as answered. Every chapter is of interest to all schools of biologists, but there is space here merely for a few of the more important conclusions. The introductory chapter on geographical distribution and dispersion is followed by chapters on variation, coloration, habits, and instincts. Of intense interest are the final chapters, entitled "Production in experiment of races, new characters, and species in Leptinotarsa," and "The problem of the origin of species." The author believes that only by such careful studies may we ever hope to find out the methods of evolution; we can never solve the problem by inspection. TOWER holds that all organic variations are responses to stimuli; "the most logical interpretation is that this variation is a response of the germ plasm . . . . due to stimuli which produce an inheritable variation differing in no respect in its transmissibility and permanency from the other variations produced." "Variation is . . . . epigenetic and not a predetermined character in organisms." Another important conclusion is that there is no fundamental distinction between fluctuating variations and mutations. TOWER secured as good illustrations of mutation in Leptinotarsa as have been obtained in Oenothera, or better, but no hard and fast lines were to be seen separating these from ordinary variations. The "mutations" differed in that the variations exhibited greater jumps, but they did not differ qualitatively. The experiments fail to support the doctrine of unit characters. In Leptinotarsa also the mutations are orthogenetic, rather than in all directions, or even in only two directions. "I maintain . . . . that mutation is not a special kind of variability . . . . but it is a part of the normal variability, and the direct response of the germ plasm to stimuli." While these experiments and the conclusions of the author thus seem out of harmony with the views of mutationists, small comfort can be obtained on the other hand by Neo-Lamarckians, for there seems to be no evidence in favor of the notion of the transmission of variations that are found to arise in the soma. Even if such variations are first visible in the soma, they are possible only when the germ plasm has developed a soma capable of variation. The botanists seem to have more generally accepted the theory of mutation than have the zoologists. It scarcely seems possible that one method has been uniformly effective in animal evolution and another as uniformly in plant evolution. Very likely nature has been more multiform in her methods than most of us have yet been willing to believe.—HENRY C. COWLES.

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[2] TOWER, W. L., An investigation of evolution in chrysomelid beetles of the genus Leptinotarsa. Carnegie Institution of Washington, Publ. no. 48. pp. 320. Washington. 1906.

Vegetable physiology

A new edition of GREEN'S *Vegetable physiology* has just made its appearance from an American press.[3] Unfortunately the author has not written any preface to the new edition and so what changes he has made can be ascertained only by laborious comparison of the new with the old. The alterations are more numerous than extensive, and it is evident that in large part the old plates are used. Yet the changes suffice for the incorporation of the more important recent advances in the science.

One of the most striking improvements is the transfer of the chapter on respiration from its former connection with the chapter on the aeration of plants to the chapter on the energy of the plant, so that it follows instead of precedes the discussion of food-making and food-getting, digestion, translocation, and storage. The topic might have received more thorough revision in its text to advantage. Other changes are noticeable in the discussion of the absorption of food materials, the chlorophyll apparatus, photosynthesis, and in the nomenclature and classification of proteids.

Not all of the slips have been eliminated in the revision, but the improvement is obvious in bringing the book more nearly up to date. The most striking defects which caught our attention are the retention of the filter theory of dialysis (at least by inference, for the explanation of osmosis is not very clear) and the statement that etiolin is converted into chlorophyll by the action of light. All the recent evidence is against both of these conceptions.

Of all parts of the book the chapters on irritability seem to us most in need of thorough reworking, but this has not been done. Perhaps the author was not free to make changes that would involve extensive resetting of type; as to this he does not take us into his confidence. By and large the book is one of the best brief texts in English that are available for elementary students. Its issue by an American house will make it much more accessible for American students.—C. R. B.

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[3] GREEN, J. REYNOLDS, An introduction to vegetable physiology. Second edition. 8vo. pp. xx+459. Philadelphia: P. Blakiston's Son & Co. 1907. $3.00.

MINOR NOTICES

The vegetation of Texas.—BRAY[4] has made a presentation in a most attractive booklet of the various ecological features of the Texas vegetation. The style of the work is popular, inasmuch as the design of the author was to make the general features of the vegetation of the state a matter of interest to students in the schools and citizens generally. First the factors of plant environment are considered, detailed application being made to the familiar plants of the state. Next follows an account of the plant societies, treated chiefly after the order of SCHIMPER. It is here especially that one may see the astonishing variety that is to be found in Texas. The woodlands range from the fine bottomland and pine forests of the southeast, through post-oak or live-oak forests to the western chaparral. Again in the mountains the characteristic conifer forests of the Rocky Mountains are to be found. There are also extensive areas of prairie and desert. Last of all is considered the vegetation of the water, halophytic areas, and dunes. It is probable that somewhere in Texas any citizen of the entire country (except the far west) could find familiar plant formations, so great is the variety. It is to be hoped that this most excellent work will be made of great use throughout the state. For the purpose it is probably the best work that any of our states possesses. There are some good maps, and a number of photographic representations of characteristic landscapes and vegetation types.—HENRY C. COWLES.

Ecological exploration in northern Michigan.—Few have recently done more to advance the frontier lines of ecology than has C. C. ADAMS,[5] and it may be said that his report on the survey of parts of northern Michigan is the record of essentially pioneer work. This is probably the first paper to extend the principles of physiographic ecology to the biota of a region. It is obvious that the future must see much work of this character, for it is only by such studies as this, carried on by a number of ecological specialists, that the complex interrelations of any biota are to be worked out. There are three special ecological papers in this report. A. G. RUTHVEN, who had charge of the field-work, under the supervision of Mr. ADAMS, presents an account of the regions studied, the Porcupine Mountains and Isle Royale. The chief feature here is the detailed description of the representative stations that were chosen for study. In each case the characteristic plants and animals are noted, and the physiographic and ecological dynamics are elucidated. Papers follow on the ecological distribution of the birds of the

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[4] BRAY, W. L., Distribution and adaptation of the vegetation of Texas. Bull. Univ. Tex. 82; Scientific Series 10. pp. 108. Austin. 1906.

[5] ADAMS, CHARLES C., An ecological survey in northern Michigan. From report of Michigan State Board of Geological Survey for 1905. pp. 133. Lansing. 1906.

Porcupine Mountains, by Otto McCreary; and on the ecological relations of the Porcupine Mountain Orthoptera, by A. P. Morse. The report is concluded by a number of annotated lists.—Henry C. Cowles.

NOTES FOR STUDENTS

A botanical survey of New Zealand.—We are constantly reminded of the remarkable vegetation of this far away-land through the indomitable energy of Cockayne,[6] whose ecological studies are always of the highest value. The island whose flora is here considered is one of the three that been has long set apart as a preserve through the commendable foresight of the New Zealand government. Perhaps the most interesting formation of the island is the forest, made up of a number of the characteristic New Zealand trees, whose distribution is related to wind in a most striking way. The heaths, the scrub, the strand, etc., are more briefly described, and then follows an interesting chapter on the affinities of the flora. The paper is accompanied with representative formation photographs, and a list of the species with Latin, English, and Maori names. The New Zealand government, which has made possible Cockayne's study of the island, and which has published this valuable report, is to be most heartily congratulated for its good sense. It is to hoped that the government will find a way to employ Cockayne's services for similar work all over the country, and especially because he is the man best fitted for this work. This is an admirable undertaking for any government, and particularly for New Zealand, since its flora is without counterpart elsewhere, and seems to be more than commonly subject to destruction by the ravages of man.—Henry C. Cowles.

Alpine flora of Argentina.—R. E. Fries[7] has given an account of some interesting Argentine plant formations, chiefly in the northwest Cordilleran region. The region as a whole is very xerophytic, and the most striking plant formation oi another type is the Hypsela formation, which is found along the stream courses, reminding one in a small way of the forest belts along streams in our prairie districts. The chief non-halophytic desert formations are the Hoffmanseggia, cactus, and Azorella formations. All are characterized by a dominance of xerophytic shrubs, but the Hoffmanseggia formation is the characteristic formation of the sandy plateaux, while the cacti dominate more on the stony hills. The Azorella formation is on the higher hills and is closely related to the cactus formation. Above the Azorella are lichen deserts. There are also regions of dunes some of which are dominated by Patagonium, others by Lampaya. Halophytic areas are extensive, some being dominated by *Salicornia pulvinata*, others by *Sporobolus arundinaceus*, and still others are shrubby areas with a dominance of

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[6] Cockayne, L., Report on a botanical survey of Kapiti Island. pp. 23. Wellington. 1907.

[7] Fries, R. E., Zur Kenntniss des alpinen Flora im nördlichen Argentinien. Nov. Act. Reg. Soc. Sci. Upsal. IV. 1:1–205. 1905.

Lepidophyllum. These chapters are followed by a discussion of the floristic and ecological relationships of the plants, a table of the species with ample taxonomic notes, and some good plates of representative plants and plant formations.—HENRY C. COWLES.

Galvanotropism again.—Miss BAYLISS,[8] working at Birmingham under the direction of EWART, has studied the effect of electric currents applied directly to roots by electrodes, polarizable and non-polarizable, and indirectly by imbedding seedlings in a 3 per cent. gelatin solution between platinum electrodes 10–12^{cm} apart. The currents used were 4.2 volts with the resistance that of the gelatin for 48 hours, or of the roots alone (3–8 minutes), or 150,000 ohms, applied for 5 to 48 hours, or 220 volts with 2220 ohms applied for 50 seconds. She finds that it makes a difference where the electrodes are placed; when on opposite sides of the sensitive (growing) region the curvature is always toward the cathode, but if one is nearer the apex than the other the curvature is toward the apical electrode. Unlike PLOWMAN, whose papers she has overlooked, she found that curvatures could be produced without injury, even by strong currents of short duration. Contrary to GASSNER, whose mode of experimentation she deprecates; she concludes that the curvatures are due to the ions produced by electrolysis and that galvanotropism therefore is a form of chemotropism, and not necessarily of traumatropism.—C. R. B.

Embryogeny in Ephedra.—*Ephedra distachya* has been studied recently by Miss BERRIDGE and Miss SANDAY,[9] who find two markedly unequal male nuclei lying in a common cytoplasmic mass. The functioning male nucleus slips out of the cytoplasmic mass and passes to the egg nucleus. Although no case of fusion was observed, fertilization is thought to occur because proembryos are found which the authors can account for in no other way than by supposing fertilization has occurred. The jacket cells arise at the same time as the central cells. Later the nuclei of the jacket cells divide by direct division, the binucleate cells enlarge and become gorged with food, and the wall of the egg breaks down, permitting the jacket nuclei to escape. The jacket nuclei fuse in pairs within the egg and give rise to proembryos. In some cases the proembryos are merely enlarged jacket cells, proembryonal cells occur within jacket cells not adjacent to archegonia, and migration and fusion of the nuclei of neighboring jacket cells precede the formation of these proembryos. These are startling claims to make in connection with the embryogeny of a gymnosperm.—W. J. G. LAND.

Items of taxonomic interest.—N. C. KINDBERG (Rev. Bry. **34**:87–92. 1907), in notes on North American mosses, has described new species under Pseudoleskeella, Hypnum (2), Dichodontium, Grimmia (2), Bryum (4), and Pohlia.—

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[8] BAYLISS, JESSIE S., On the galvanotropism of roots. Annals of Botany **21**: 387–405. *figs. 6.* 1907.

[9] BERRIDGE, ETHEL M., and SANDAY, ELIZABETH, Oogenesis and embryogeny in *Ephedra distachya*. New Phytologist **6**: 128–134, 167–174. *pls. 3, 4.* 1907.

M. L. Fernald (Rhodora 9:140–146. 1907), in a presentation of the genus Suaeda in northeastern America, recognizes 4 species and describes one as new (*S. Richii*).—G. F. Atkinson and C. W. Edgerton (Jour. Mycol. 13:185, 186. 1907; also Science N. S. 26:385, 386. 1907) have published a new genus (*Protocoronospora*) of fungi discovered infecting the cultivated vetch, and have published it in two journals without any evidence as to which publication is to be regarded as the original one.—C. H. Peck (Bull. Torr. Bot. Club 34:345–349. 1907) has described 12 new species of fleshy fungi, distributed among 8 genera.—E. Hassler (Bull. Herb. Boiss. II. 7:718–740. 1907), in continuation of his *Plantae Paraguariensis*, publishes a new genus (*Paradolichandra*) of Bignoniaceae.—L. Radlkofer (Leaflets Philippine Bot. 1:208–211. 1907) has published 4 new species of Sapindaceae from the Philippines.—J. M. C.

Movement of water.—Dixon adduces experimental evidence[10] that Ewart's estimates[11] of the velocity of the transpiration stream and the resistances it encounters are vastly too great. Ewart calculated from his data that it would require a head of water 6–33 times the height of the tree to drive a sufficient amount of water against the resistance encountered. According to Dixon's data, with liberal allowances for transpiration, it would suffice to have a head equal to the height of the tree. As to the soundness of the cohesion theory of the ascent of water, against which Ewart had brought his conclusions as objections, Dixon says: "Apart from the weighty evidence which has elsewhere been adduced in its favor, the fact that other theories, both old and new, have to assume properties for the waterways of plants which are either in the highest degree improbable . . . . or are even directly negatived by experiment, seems to support the theory by a process of exclusion."—C. R. B.

Light perception.—Another adverse report on Haberlandt's theory of the lens-function of the epidermal cells in the perception of light is rendered by Nordhausen.[12] Unlike Haberlandt, who obliterated the lens action by a film of water, and Kniep who reversed it by paraffin oil, Nordhausen used a film of 5–10 per cent. gelatin, whose refractive index is almost that of cell contents. (By making the gelatin opaque with lamp black he used it also to exclude light from the petiole, for which it is much superior to leather or paper.) He found that the clear gelatin did actually eliminate the lens action of the convex cells, and testing the ability of the leaf to respond to light in the very plants used by HABERLANDT, he reports uniformly positive results, both with and without the darkening of the petiole; whence he concludes that "the lens-function does not stand in direct causal connection with the perception of the direction of light by the leaf-blade."—C. R. B.

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[10] Dixon, H. H., On the transpiration current in plants. Proc. Roy. Soc. London B. 79:41–57. 1907.

[11] Ewart, A. E., Ascent of water in trees. Phil. Trans. Roy. Soc. London B. 198:41–85. 1905. Also, The resistance to flow in wood vessels. Annals of Botany 19:111. 1905.

[12] Nordhausen, M., Ueber die Bedeutung der papillösen Epidermis als Organ für die Lichtperception des Laubblattes. Ber. Deutsch. Bot. Gesells. 25:398–410. 1907.

Branching in palms.—In 1892 MORRIS[13] brought together what had been recorded concerning the branching of palms, which was regarded as an abnormal phenomenon. RIDLEY,[14] who has had eighteen years of experience in the oriental tropics, has now much extended our knowledge of this phenomenon. He believes that the greater number of palms are branched at least at base, and that the production of a single axis from a seed may be regarded as the "abnormal" condition. Lateral buds are produced at or near the base, and these become erect stems, in some cases the whole plant eventually becoming a bush; or these lateral buds may develop as subterranean branches that send up a succession of erect stems (branches). Heretofore the branching of palms has been thought of only in connection with the crown, but RIDLEY'S observations indicate that the group is perhaps characterized by a tendency to basal branching.—J. M. C.

Spirogyra.—Dr. FRITSCH and Miss RICH[15] have begun a series of studies of the British freshwater algae, the first one dealing with Spirogyra. The principal topics are: "The occurrence of Spirogyra in nature," "The reproduction of Spirogyra in nature," and "Points of systematic interest." The species examined were either purely vernal or exhibited both a vernal and an autumnal phase. The autumnal appearance of certain species is thought to be due to certain external conditions that cause a small number of zygospores to germinate. "Reproduction takes place ordinarily in the vernal phase, and is most probably the result of certain periodically recurring combinations of factors, which vary for different species;" in support of which view the authors present a considerable number of data.—J. M. C.

Limiting factors and growth.—A. M. SMITH, late a pupil of BLACKMAN at Cambridge, has carried out a thorough study of the rate of growth in a number of plants at different stations in Ceylon, applying to the discussion of his results[16] BLACKMAN'S fruitful theory of limiting factors. In Agave and Furcraea temperature (probably the internal temperature of the growing parts) always was the limiting factor, while in Dendrocalamus sometimes the water supply, sometimes the temperature was limiting. In Capparis and Stifftia it seems to be the water supply by day and temperature by night; in Vitis the temperature in January, and the water supply in July. The paper is a most suggestive one. It seems quite likely the conflicting data on growth can be harmonized by further study along this line.—C. R. B.

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[13] MORRIS, DANIEL, On the phenomena concerned in the production of forked and branched palms. Jour. Linn. Soc. London Bot. **29**:281. 1892.

[14] RIDLEY, H. N., Branching in palms. Annals of Botany **21**:415–422. *pls. 34–39.* 1907.

[15] FRITSCH, F. E., and RICH, FLORENCE, Studies on the occurrence and reproduction of British freshwater algae in nature. I. Preliminary observations on Spirogyra. Annals of Botany **21**:423–436. 1907.

[16] SMITH, A. M., On the application of the theory of limiting factors to measurements and observation of growth in Ceylon. Annals Roy. Bot. Gardens Peradeniya **3**:303–375. *pls. 22–25.* 1907.

Infectious chlorosis.—BAUR[17] reports that the variegated forms of *Ligustrum vulgare*, *Liburnum vulgare*, *Fraxinus pubescens*, *Sorbus aucuparia*, and *Ptelea trifoliata*, which are propagated by cuttings, owe their yellow or variegated leaves to an infectious chlorosis like that recently described in detail for *Abutilon Thompsoni*. A yellow variety of *Ptelea trifoliata*, however, which can be grown from seed, is a true *aurea*-form, and its condition is not transmissible by infection. BAUR expects to find this disease widespread, when time avails for examining the many wild and commercial variegate-leaved plants. He intends to make his next task the isolation of the problematic infecting material.—C. R. B.

The primary uredospore.—CHRISTMAN[18] has investigated the development of the so-called primary uredospore of *Phragmidium potentillae canadensis*. He brings out the resemblance between the true aecidium and the primary uredo, the spores in the two cases being morphological equivalents. The relation of these results to the life-history as a whole is presented in a later paper published in this journal.[19]—J. M. C.

Anaerobic respiration.—STOKLASA and his collaborators[20] report further successful isolation of the enzymes which in the absence of oxygen break up carbohydrates in plant cells into lactic acid, and then into alcohol and CO_2. Zymase is responsible for the lactic acid; lactacidase for the alcoholic fermentation, with hydrogen as a by-product. This seems indirectly to support POLLACCI'S hypothesis that in photosynthesis we have reduction of CO_2 by H.—C. R. B.

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[17] BAUR, ERWIN, Ueber infektiöse Chlorosen bei Ligustrum, Laburnum, Fraxinus, Sorbus, und Ptelea. Ber. Deutsch. Bot. Gesells. **25**:410–413. 1907.

[18] CHRISTMAN, A. H., The nature and development of the primary uredospore. Trans. Wis. Acad. Sci. **15**:517–526. *pl. 29*. 1907.

[19] CHRISTMAN, A. H., Alternation of generations and the morphology of the spore forms in rusts. BOT. GAZETTE **44**:81–101. *pl. 7*. 1907.

[20] STOKLASA, ERNST, and CHOCENSKÝ, Ueber die anaerobe Atmung der Samenpflanzen und über die Isolierung der Atmungsenzyme. Ber. Deutsch. Bot. Gesells. **25**:122–131. 1907.

NEWS

Dr. Raymond H. Pond, recently of the New York Botanical Garden, has sailed for Germany, to study under Pfeffer at Leipzig.

Dr. Richard Wettstein, Vienna, has been elected president of the "Association of German Men of Science and Physicians," to meet next year at Cologne.

Dr. Ezra Brainerd, well known among botanists for his work on the flora of Vermont, has resigned the presidency of Middlebury College, an institution which he has served for 43 years.

The *Bryologist* for November offers the usual interesting fascicle of notes on mosses, liverworts, and lichens. The brief contributions of many observers and students of these plants are of real service.

Professor J. Behrens has been called to the directorship of the biological Experiment Station at Berlin-Dahlem (the seat also of the Imperial Botanic Garden), as successor to the late Professor R. Aderhold.

J. Arthur Harris, Missouri Botanical Garden, has been appointed on the staff of the Carnegie Station for Experimental Evolution at Cold Spring Harbor, to succeed E. N. Transeau, now at the State Normal School, Charleston, Illinois.

Professor Ludwig Jost, of the University of Strassburg, has been called to the State Agricultural College at Bonn-Poppelsdorf and to an assistant professorship in the University of Bonn, as successor to Dr. Fritz Noll, who went to Halle.

In the September number of the *Chautauquan*, a series of articles, entitled "Some great American scientists," begins with a biographical sketch of Asa Gray, by Professor C. R. Barnes. The frontispiece of the number is a portrait of Dr. Gray.

Mr. A. H. Curtiss, the well-known collector of plants from the southeastern United States and West Indies, whose sets are widely distributed and highly prized in the herbaria of the world, died at his home in Jacksonville, Florida, September 1, at the age of 62 years.

J. E. Kirkwood, formerly of Syracuse University, has been appointed assistant botanist to the Mexican-Continental Rubber Company, whose laboratory is at Hacienda de Cedros, Mazapil, Zacatecas. It is in this company that Francis E. Lloyd is director of investigation, with the same laboratory address.

Clark Hall, of the Massachusetts Agricultural College, the new building named after Colonel William S. Clark, an enthusiastic botanist and one of the first presidents of the institution, was dedicated on October 2. Addresses were given by Professor D. P. Penhallow, McGill University, on "William Smith Clark: his place as a scientist and his relation to the development of scientific agriculture;" and by Professor John M. Tyler, Amherst College, on "Reminiscences of Colonel W. S. Clark."

GENERAL INDEX

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.

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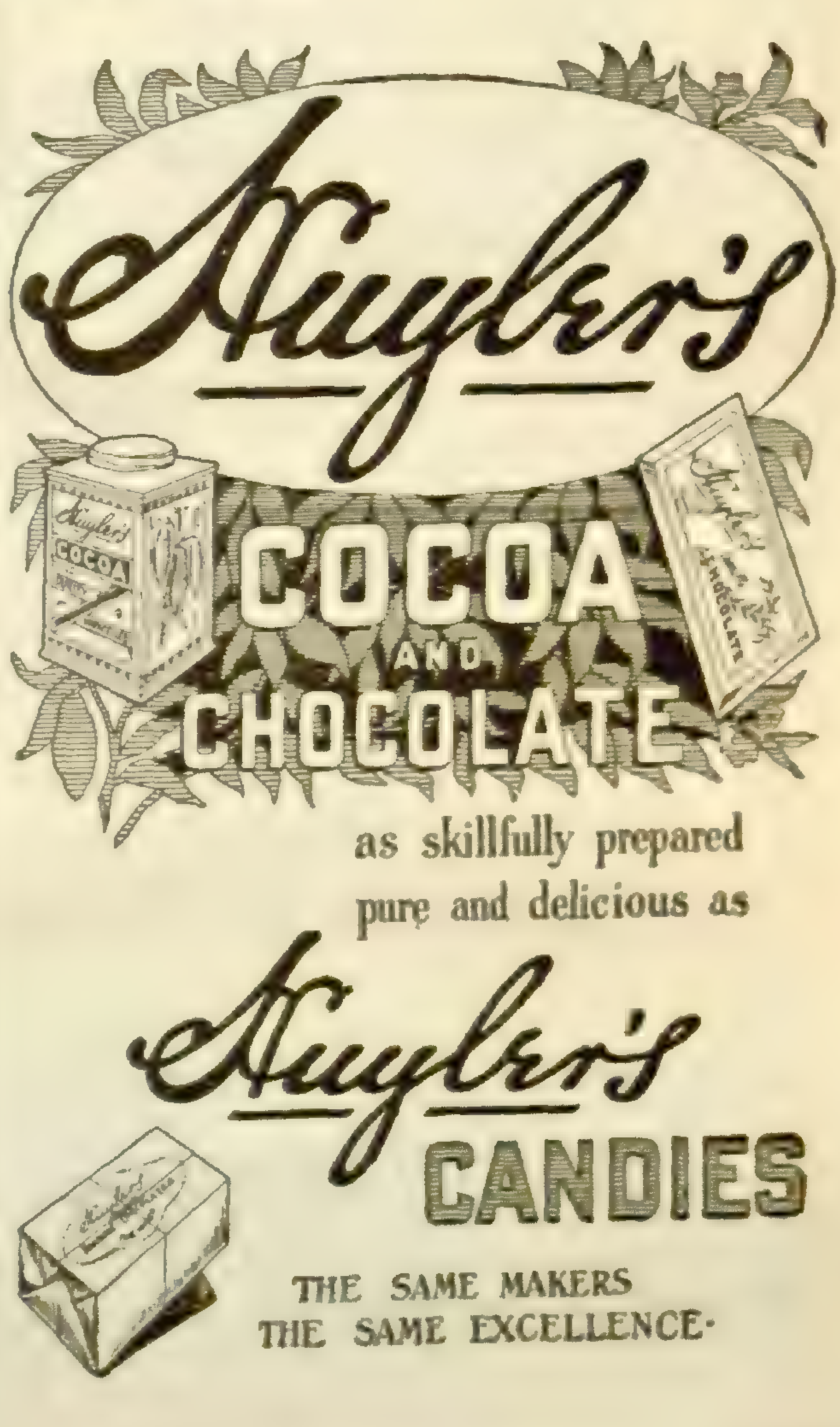

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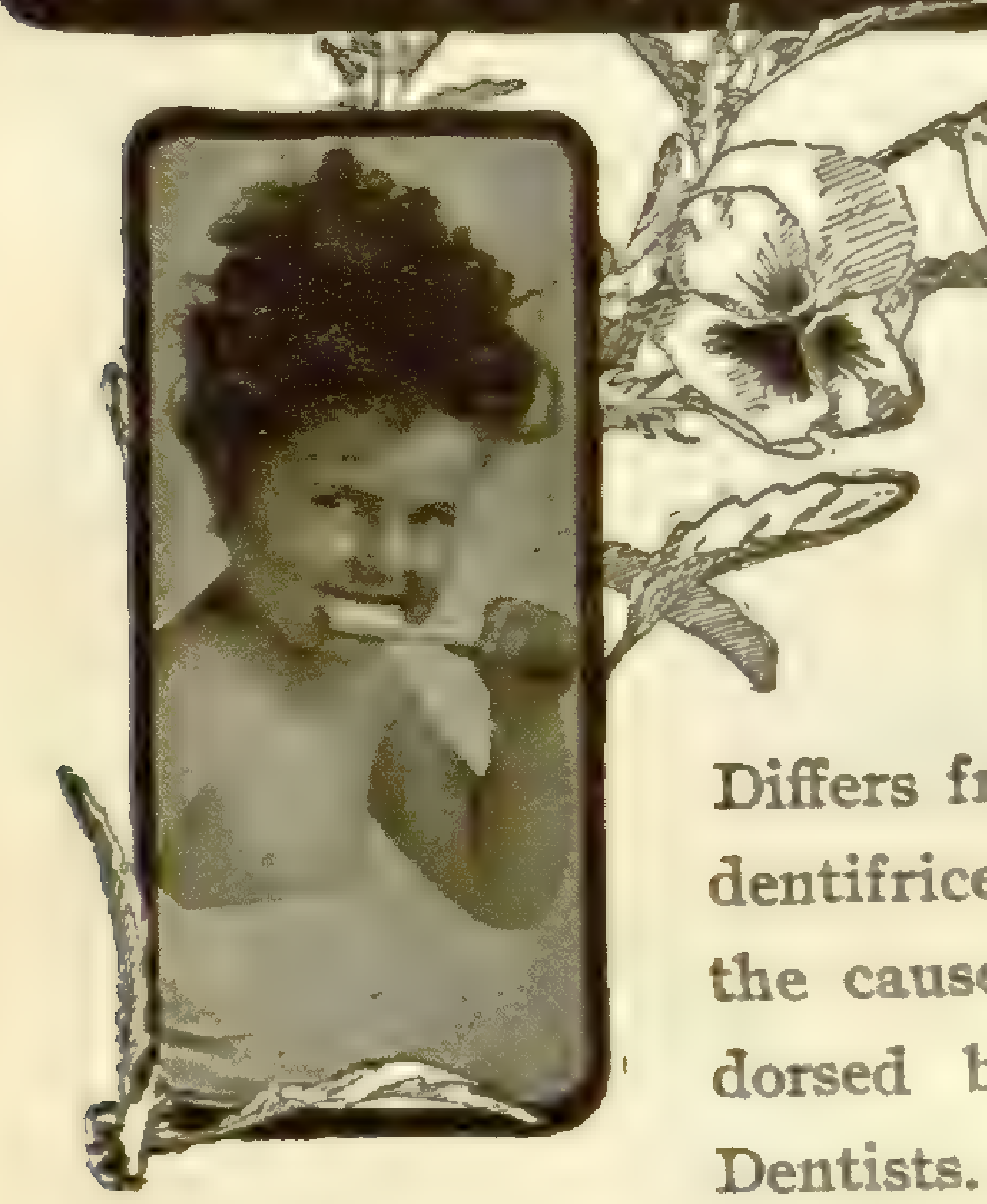

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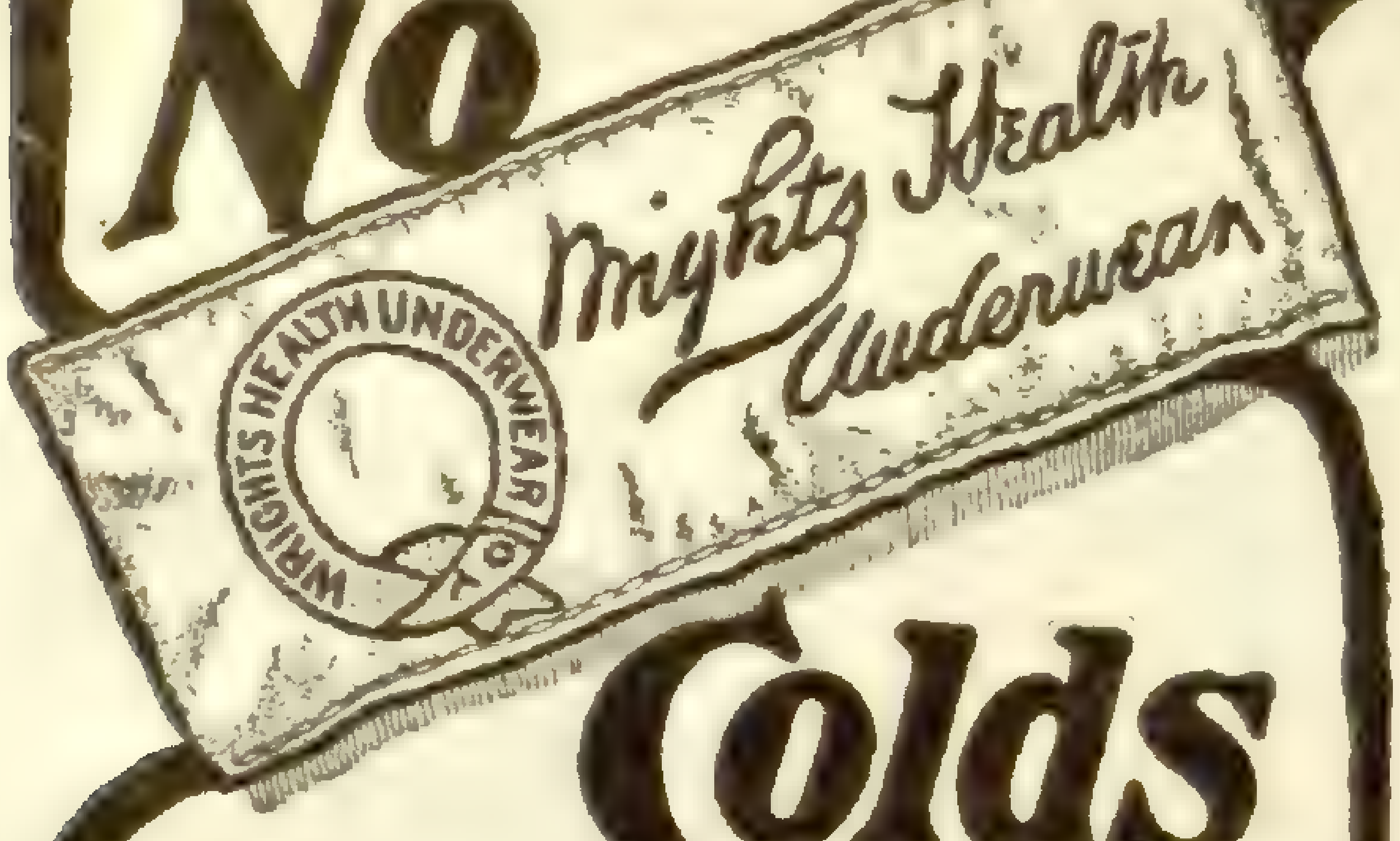

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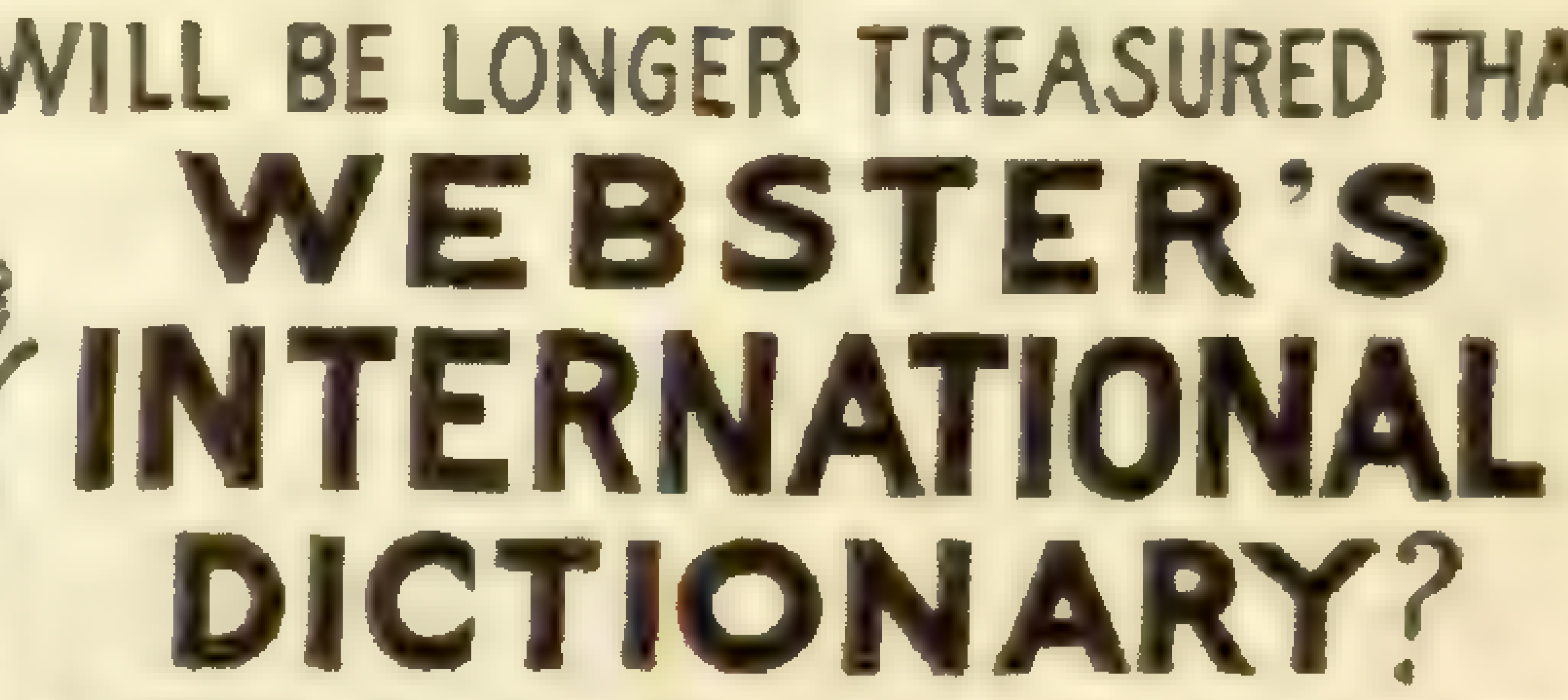

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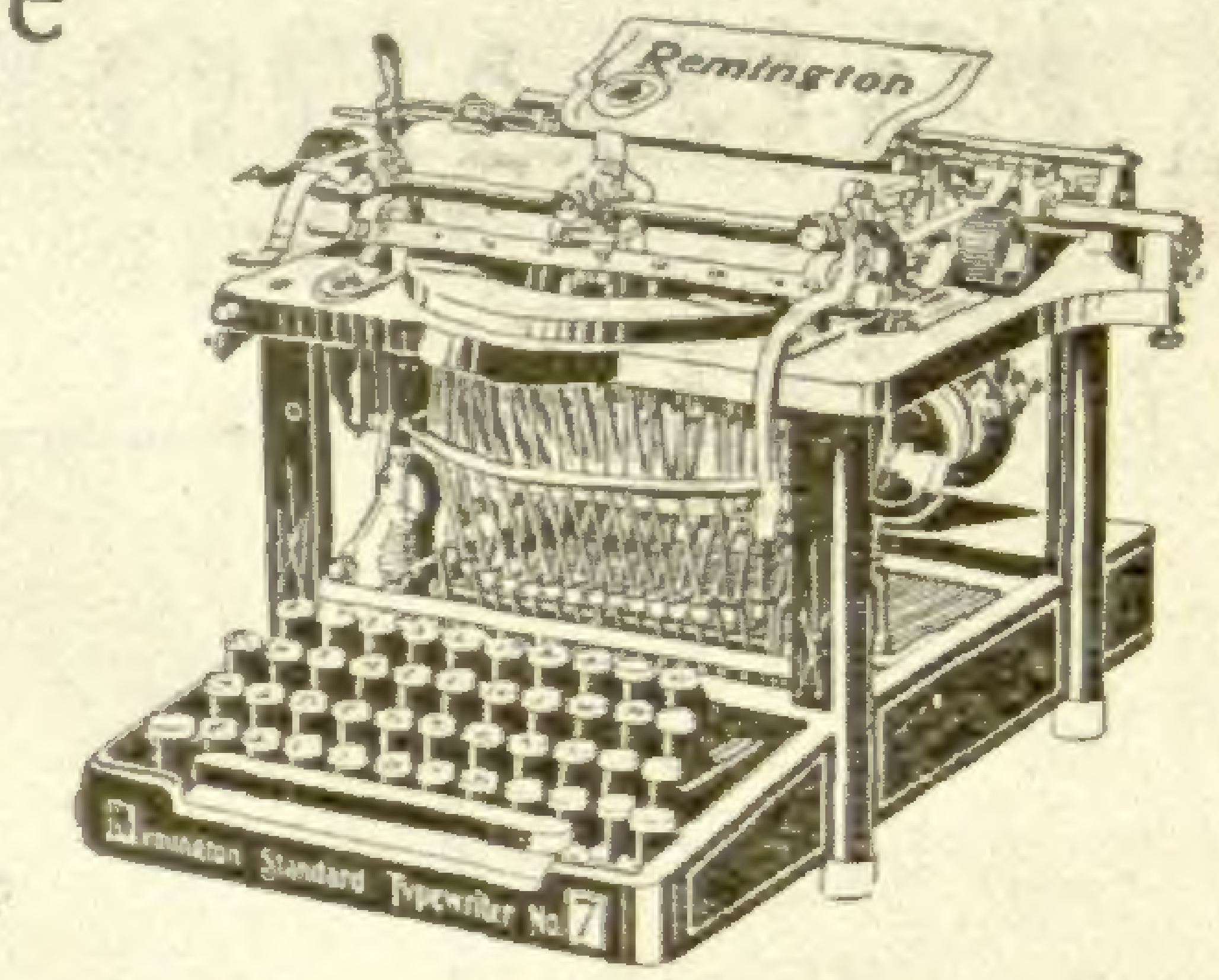

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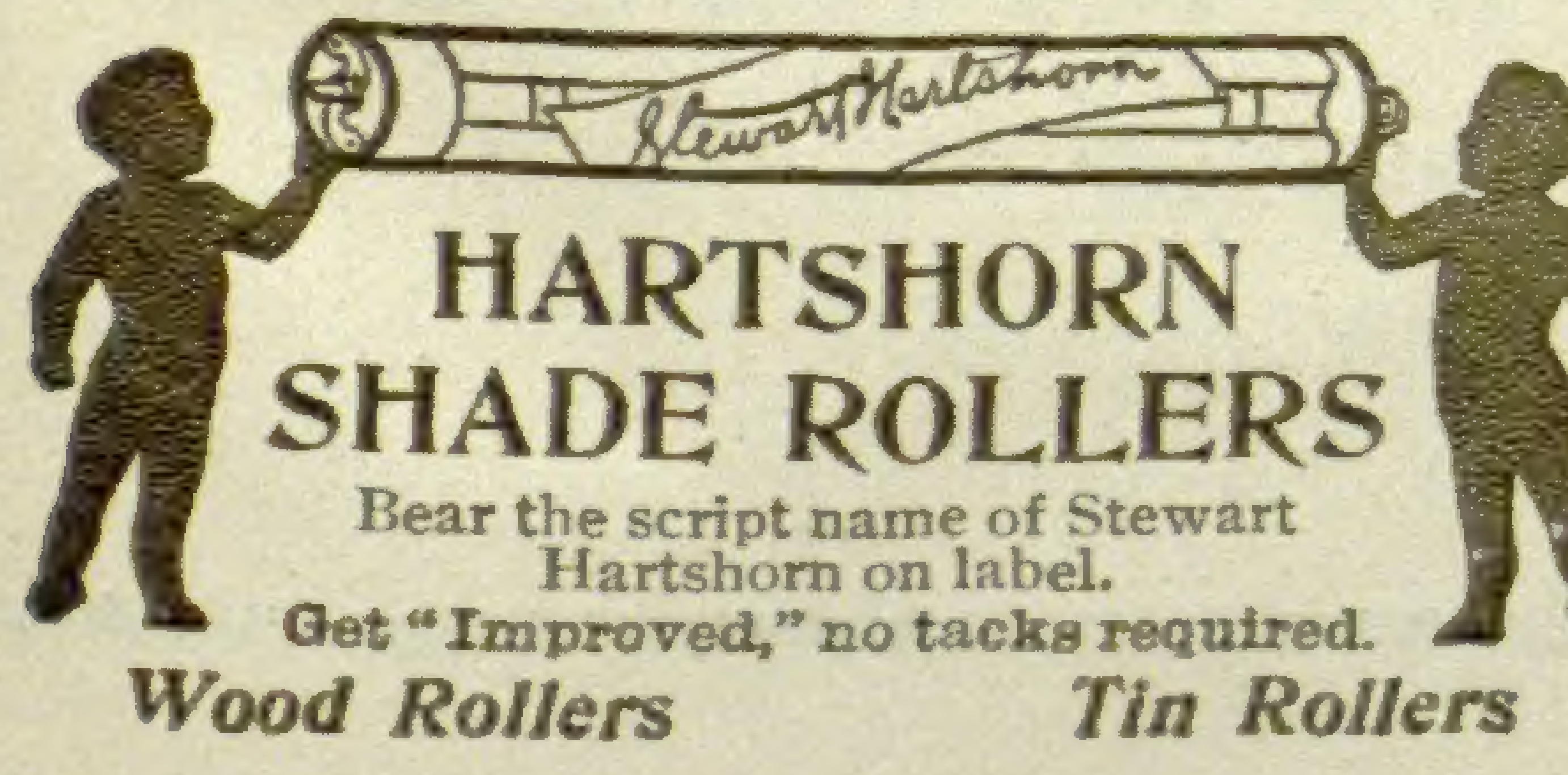

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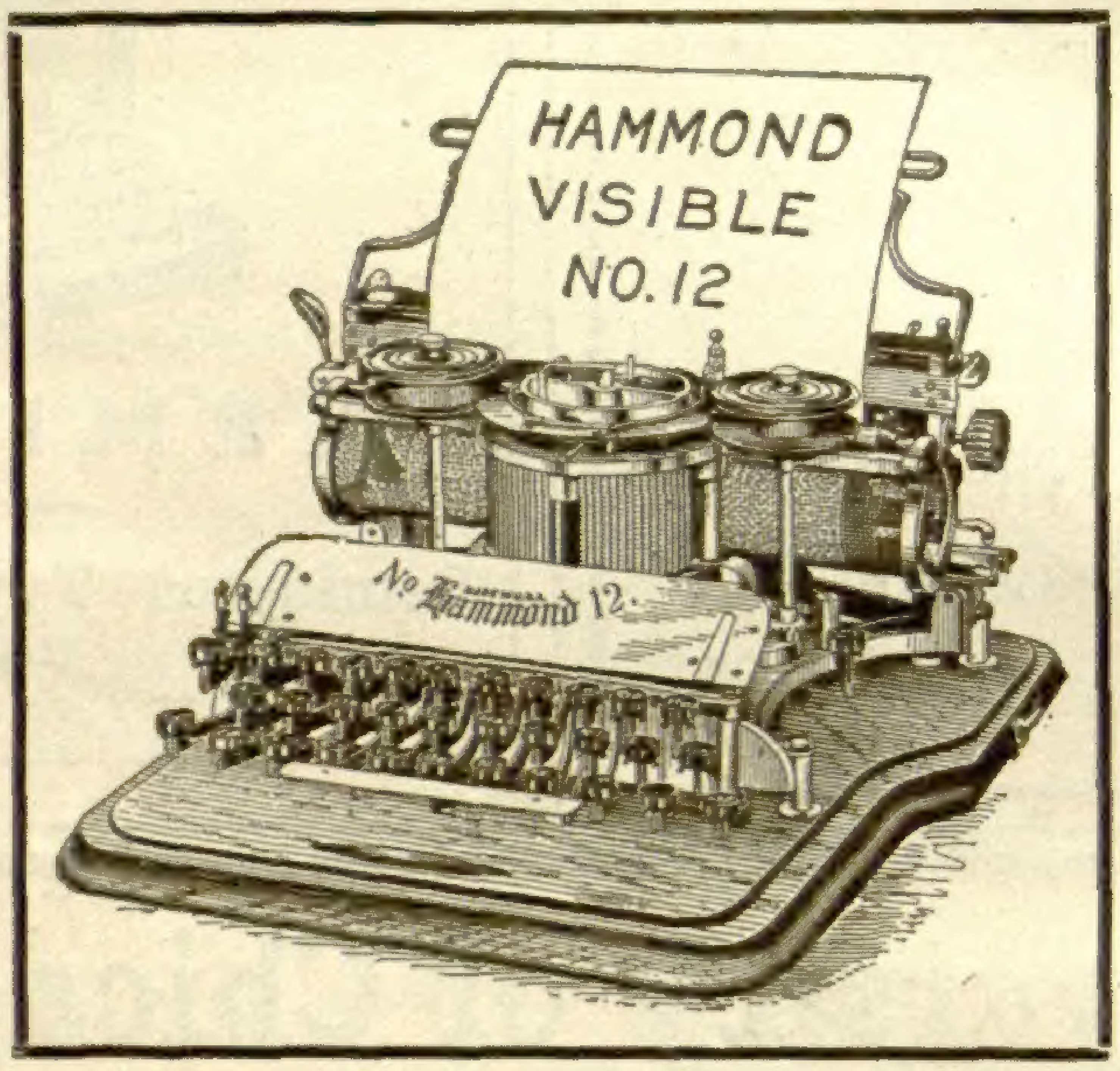

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